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Fisheries Ecology Program (FEP): General Introduction[1]

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(J9939)

It is a truism that fisheries production depends on oceanographic conditions, yet it seems that improvements in our ability to explain the variance of fisheries yield in terms of oceanographic indicators must always be bought at the cost of great additional efforts. Each forward step demands ever more extensive surveys, longer time-series, and increased resolution of the measurements. In 1982, in the attempt to better understand the provision of sound management advice, a number of scientists from various government and university laboratories of the Canadian Atlantic oceanographic community joined forces to examine current sampling requirements for investigating aspects of biological production and related physical processes on the Scotian Shelf. The western shelf in the vicinity of Browns Bank (NAFO Subarea 4X) was selected as the area for studying factors affecting the economically important gadoid fisheries, particularly haddock. The activity, which became known as the "Fisheries Ecology Program" (FEP), required a multidisciplinary approach including physical oceanography, and primary and secondary production as well as the dynamics of the fish and the fishery itself. The product is the result of commitments of effort by the scientists for a period of 3 yr (1983–85) to a cooperative series of field, laboratory, and review studies. During this time the studies have been supplemented by periodic reviews to compare ideas and results and to make plans for future work.

The following group of six papers represents an initial sampling of results from this venture. The groundwork for the study was laid by defining both the persistent patterns and low frequency variations in the physical oceanographic system as they respond to tidal, wind, topographic, and seasonal forcing (Smith). Rates of dispersion of drifting particles in the surface layer were found to have time scales comparable with those of a number of important biological events, particularly among the smaller particle sizes and in the early life-histories of the fish. The studies of the zooplankton production (MacLaren et al.) and benthic macrofaunal production (Wildish et al.) show that events at these stages of the food chains are clearly keyed to phenomena at the topographical and seasonal scales, but, at least in the benthic fauna, they seem to be additionally linked with the higher levels of the food chains by mechanisms and energies provided by persistence of forces at smaller scales, such as the tides. Among fish eggs and larvae it is perhaps not a surprise to find that the growth, survival, and distribution are affected by the oceanographic regime at various scales; however, it is clear (Suthers and Frank) that the distribution could not have been deduced without taking into account the bias that can be imposed by the strong size-selectivity of a single sampling gear. The results of sampling with the combination of nets showed that interannual changes in larval cod distributions in relation to vississitudes in water movements at the smaller time and space scales provide a potentially powerful mechanism for explaining differences in year–class success in the fishery.

The results of the larval and juvenile sampling in relation to the smaller scales of water movements (Suthers and Frank) also clearly show that the patterns of distribution at successively later stages in the early life history are modified by behaviour so that it becomes important to understand at what stages and with what power this capacity of the organisms for adjustment in relation to water motions is developed. Capacity for behavioural adjustment also appears necessary to explain the conclusion from the larval growth studies (Campana and Hurley) that while the organisms are responsive to temperature, the models do not require a food density term. The effective density of food is evidently a parameter over which larvae may exercise some control through adjustments of local spacing. In a similar vein the study of the fisheries yield (Boudreau and Dickie) suggests that regularities in adult fish production in relation to their size depend on their capacity to adjust their densities in response to short term food density changes. What has not been evident heretofore is the conclusion that adjustments that had been deduced as taking place at the level of species behaviour are apparently mediated by graded behavioural changes throughout the life history of individual cohorts.

This publication is seen as the first offering of individual results of our cooperation. Even at this stage we can take some satisfaction in the fact that this new knowledge of scaling factors improves our ability to explain and predict future production from physical indicators more efficiently than before. While this is one of the most important practical goals in the science, we anticipate that future publications will involve a synthesis of the individual efforts through comparisons and modelling developed with combined data sets. It is our belief that the increased understanding derived from the FEP scientific results provides a basis for improved advice for fisheries management.

[1]This is part of a series of papers devoted to the Fisheries Ecology Program.

Circulation and Dispersion on Browns Bank[1]

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Smith, P. C. 1989. Circulation and dispersion on Browns Bank. Can. J. Fish. Aquat. Sci. 46: 539–559.

Year-long current measurements reveal a permanent clockwise gyre over the western cap of Browns Bank. Maximum mean currents (0.25 $m \cdot s^{-1}$) over the steep northern flank are uniform in the upper water column, except when pulses of low salinity water arrive from the Scotian Shelf producing stratification and vertical shear. Significant off-bank Eulerian mean currents, found near the bottom on the 100-m isobath, are consistent with the models for topographic interactions of the semidiurnal tides. A multiple regression analysis in the spectral domain reveals most low-frequency energy is concentrated in the 14–28-d bands where wind- and tidally-forced currents make roughly equal contributions (30–40%) to the total variance. In the synoptic bands (2–10-d), wind forcing alone contributes 60–80% of the variance. The temporal and spatial variability of the gyre is supported by satellite-tracked drogue studies on the Bank in three seasons. April and November 1983 observations show that the gyre circulation may be broken down by wind-forced currents. In July/September 1983, drogues consistently exited the western cap of the Bank from the northern flank after a residence time of 14 d, comparable with the near-surface recirculation time. Isotropic dispersion coefficients ($30 \leq K_H \leq 160$ $m^2 \cdot s^{-1}$) are found to follow Okubo's (1971) empirical formulae.

La mesure des courants sur un an, révèle la présence d'un tourbillon permanent qui circule en sens horaire au-dessus de la partie occidentale du banc Browns. Les courants moyens maximum (0,25 $m \cdot s^{-1}$) au-dessus du flanc nord abrupt sont uniformes dans la colonne d'eau supérieure, sauf lorsque de l'eau de faible salinité en provenance du plateau Scotian produit une stratification et un cisaillement vertical. On a découvert au large du banc et près du fond sur l'isobathe de 100 m, d'importants courants moyens eulériens qui sont conformes aux modèles d'interactions topographiques des marées semi-diurnes. Une analyse de régression multiple dans le domaine spectral montre que la majeure partie de l'énergie de basse fréquence est concentrée dans les bandes de 14–28-d au cours desquelles les courants engendrés par le vent et poussés par les marées contribuent à peu près également (30–40 %) à la variance totale. Dans les bandes synoptiques (2–10 d), le vent seul contribue à 60–80 % de la variance. La variabilité temporelle et spatiale du tourbillon a été montrée par des études de drogues suivies par satellite réalisées sur le banc au cours de trois saisons. En avril et novembre 1983, les observations montrent que la circulation du tourbillon peut être interrompue par des courants engendrés par le vent. Entre juillet et septembre 1983, les drogues ont invariablement dépassé le cap occidental du banc en provenance du flanc nord après un « temps de résidence » de 14 d, comparable à la période de recirculation qui existe près de la surface. Les coefficients de dispersion isotrope ($30 \leq K_H \leq 160$ $m^2 \cdot s^{-1}$) sont conformes aux formules empiriques d'Okubo (1971).

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The economic and social importance of the Browns Bank fisheries led to a proposal to conduct a multidisciplinary investigation (The Fisheries Ecology Program or FEP) of the factors affecting the productivity of haddock (*Melanogrammus aeglefinus*) in the waters off Southwest Nova Scotia (North Atlantic Fisheries Organization Subarea 4X). Based on tagging studies, research trawl and ichthyoplankton surveys, 4X haddock is believed to be a discrete stock with high but extremely variable recruitment. Spawning occurs primarily in the late spring (April–May) on various areas of the Bank, but subsequent surveys have indicated large concentrations of eggs and larvae distributed over the surrounding region. This observation raises questions regarding the roles of horizontal advection and dispersion in retaining the buoyant plankton on the Bank during the critical phases of their early life history. Of particular interest are (1) the integrity of the clockwise gyre over the western cap of Browns in the face of strong wind forcing and (2) the effective residence time for buoyant particles in the surface layers. One historical hypothesis is that frequent breakdown of the gyre during a particular spawning season would reduce the residence time on the Bank and adversely affect the survivability of that year–class. However, interpretation of some of the measured distributions of haddock eggs and larvae and their associates (prey and predators) during FEP (K. Frank, P.O. Box 1006, Dartmouth, N.S. B2Y 4A2, pers. comm.) suggests that passive transport of early-stage gadids from the Bank to the inshore region (where prey of appropriate size are abundant) actually enhances survivability. In this case, retention on the Bank would be detrimental.

To examine the issues of circulation and dispersion in the surface layers, a physical oceanographic field program focussed on Browns Bank was conducted from April 1983 – May 1985 to complement the biological program of FEP. The oceanographic background for this study is given in the next section, followed by a description of the experiment and a discussion of the salient results.

[1]Fisheries Ecology Program Contribution Number: 1.

Background

The presence of topographic irregularities, such as shallow submarine banks, has a pronounced effect on the mean and transient circulations on the continental shelf. Vorticity constraints tend to guide the mean currents along bathymetric contours and produce horizontal gradients in the flow which are consistent with topographic length scales. Furthermore, these effects can be magnified in regions of energetic tidal currents where mechanisms such as tidal rectification (Loder 1980) may drive strong mean currents along isobaths. A recent investigation of the circulation on Georges Bank in the Gulf of Maine (Butman et al. 1982) reveals some characteristic features of bank circulations, such as the dominance of a permanent clockwise gyre with maximum currents located over the steeply sloping flank regions. Moreover, the intense semidiurnal tidal currents over the top of the bank produce strong vertical mixing which leads to sharp horizontal gradients in density and stratification (Garrett et al. 1978) that support a baroclinic circulation (Garrett and Loder 1981). The presence of stratification can considerably complicate the relationship between the tidal, low-frequency, and mean currents. Magnell et al. (1980), for instance, found high coherence between the amplitude of the semidiurnal tidal current and the wind-driven (periods of 3–5 d) along-isobath component of the subtidal circulation on the northern slope of Georges Bank. From this they concluded that a local nonlinear interaction links the tidal and low-frequency currents, with both steep bottom topography and density structure as important factors. Ou and Maas (1986) have since demonstrated that the mean transverse (i.e. cross-isobath) circulation driven by buoyancy fluxes associated with either the (viscous) barotropic or baroclinic tide on a steep slope is characterized by strong off-bank flow near the bottom as observed by Magnell et al. (1980).

The interaction of strong, vertically-sheared tidal currents with the residual current associated with small scale topographic irregularities may also result in enhanced horizontal dispersion on the top of a bank (Loder et al. 1982) through a rectification process described by Zimmerman (1980). This physical mechanism involving a cascade of shear dispersion processes may easily result in effective horizontal dispersion coefficients in the range of 100–1000 $m^2 \cdot s^{-1}$. However, as pointed out recently by Zimmerman (1986), it is presently impossible to distinguish between the shear dispersion mechanism and "Lagrangian chaos," in which genuine hydrodynamic turbulence is absent but particle trajectories become random functions of time that diverge in a form of "tidal random walk" or as a result of spatial randomness in the Eulerian velocity field. Regardless of the mechanism, however, the high rates of horizontal dispersion which characterize these energetic tidal regimes have important implications for the biological productivity of the bank.

Off Southwest Nova Scotia, moored current meter measurements (The Cape Sable Experiment; Smith 1983) have provided evidence for a permanent clockwise gyre around the shallow western cap of Browns Bank. Using coherent modulations at monthly and fortnightly periods between low-frequency current components and the major axis amplitude of the semidiurnal tidal stream, Smith estimated the strength of the tidally-induced component on the northern flank of the Bank and concluded that a substantial fraction of the gyre circulation is tidally driven. This result is qualitatively consistent with 2- and 3-D model calculations (e.g. Tee et al. 1987). It is noteworthy that, in contrast to the observations of Magnell et al. (1980) on the north slope of Georges Bank, the modulations of the tidal amplitude showed no significant variability in the dominant wind-driven bands (periods 3–5 d) suggesting that the wind-baroclinic tide coupling does not play a role in the rectification process on Browns Bank. On the other hand, Wright et al. (1986) used observations and a numerical model to demonstrate that the depth-averaged steady-state response to longshore wind stress over the Bank consists of a broad current in roughly the same direction but guided to some extent by coastline and topography. The response to cross-shore wind was found to be much weaker.

Smith (1983) also showed that the seasonal cycle in hydrographic properties off Cape Sable is controlled, in part, by the arrival late in the year (e.g. November) of a pulse of low salinity water from the Gulf of St. Lawrence and that spatial gradients in the density field resulting from that phenomenon and local mixing play an important role in the dynamics of the mean circulation. Using a high resolution numerical model, Loder and Greenberg (1986) have recently predicted a well-mixed zone over the western cap of Browns Bank under several alternate hypotheses regarding the physical mechanism for mixing.

Another component of the Cape Sable Experiment involved a study of the Lagrangian near-surface circulation using drogued satellite-tracked drifters (Trites 1980). The tracks of these buoys tended to confirm the existence of a clockwise gyre around Browns Bank, but also showed some response to wind. Those released in the vicinity of the Bank remained within 25 km of the 100-m isobath for periods ranging from 5 to 65 d.

The results of the Cape Sable program formed the basis for designing the Browns Bank Experiment as part of FEP.

Browns Bank Experiment

The main components of the experimental program consisted of:

(1) an array of moored current meters at various sites on Browns Bank and off Cape Sable,
(2) seasonal hydrographic surveys of the area, and
(3) several small-scale dispersion studies at various locations on the Bank using clusters of satellite-tracked drogued drifters.

The mooring array (C2–C3, C7–C10; Fig. 1) was designed to investigate the structure and dynamics of the clockwise gyre on the western cap of Browns and to monitor the low salinity inflow to the region from the Scotian Shelf. Moorings C2 and C3 (slightly relocated) were part of the original Cape Sable array while C7 and C8 were placed on the same isobath (110 m) on the northern and western flanks, respectively. C9 monitored conditions on the shallow cap of the Bank and C10 was placed between C9 and C3 on the 70-m isobath. Four of the six moorings were placed in April 1983 and the full array was moored for the winter/spring period of 1984. Subsequently, only single moorings remained in place to monitor conditions in the inshore zone (C2) and on the Bank (C10).

The primary moored instrument was the Aanderaa RCM-5 current meter set to sample at 30-min intervals. The estimated accuracies of the Aanderaa speed ($\pm 1.3\%$ caused by intrinsic rotor error at speeds over 0.2 $m \cdot s^{-1}$ or ± 5 $mm \cdot s^{-1}$ for speeds between threshold and 0.2 $m \cdot s^{-1}$; Tang and Hartling 1979), direction ($\pm 5°$; Keenan 1979) and temperature ($\pm 0.04°C$; Boyce 1982) sensors were determined from laboratory calibrations. However, a major problem with fouling of the conduc-

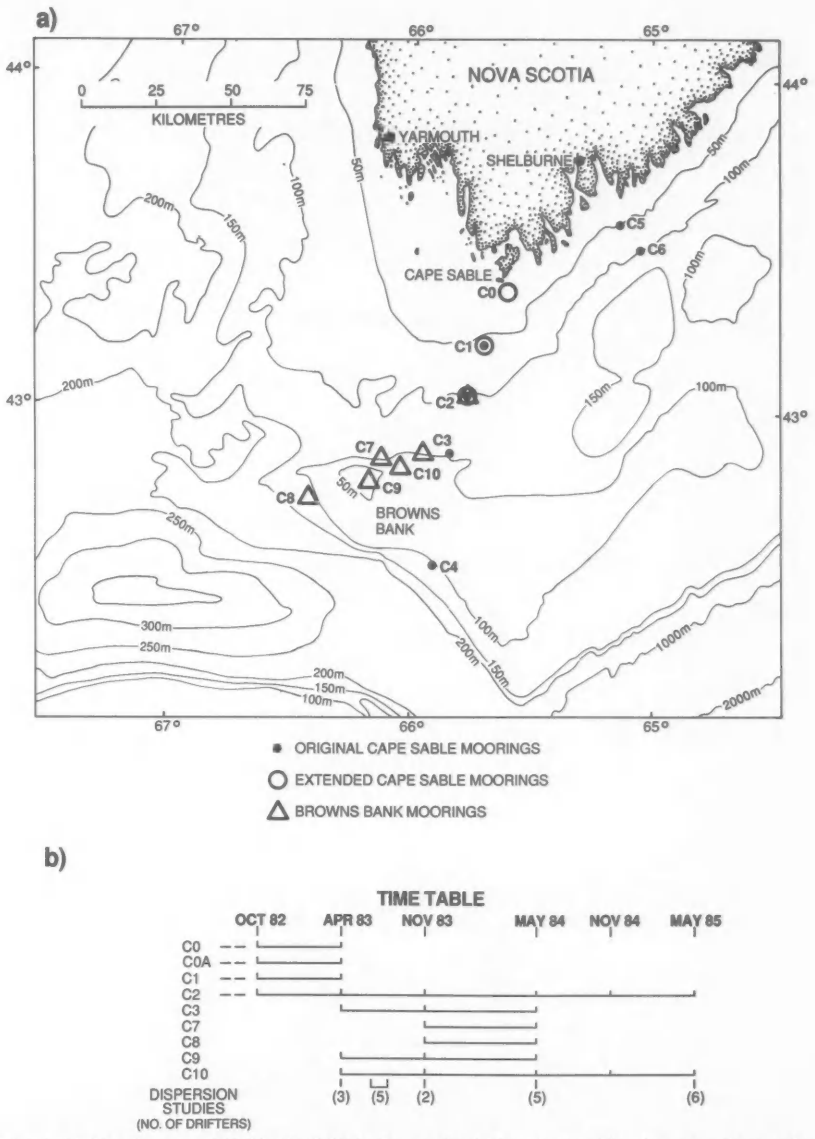

FIG. 1. (a) Mooring array (C2,C3,C7–C10) for Browns Bank Experiment. Also shown are the mooring arrays for the original Cape Sable Experiment (C1–C6) conducted in 1978–80 and the Extended Cape Sable Experiment (C0–C2) from 1980–83. (b) Time table for Browns Bank Experiment.

tivity sensors was discovered during postrecovery shipboard calibrations that rendered the salinity records for all deployments prior to May 1984 useless. The salinity time series suggested that the calibration degraded most severely over the latter portions of the records with typical salinity errors (current meter-standard) of -0.2 to -1.2 on recovery. This problem was remedied with the May 1984 deployment by applying antifoulant paint to the conductivity cells which reduced the post-deployment calibration errors to within ± 0.10.

Each mooring (except C9) contained at least three instruments: near the surface ($\approx$15 m), bottom (10 m above) and at mid-depth. The northern slope moorings (C3, C7) included an additional instrument between surface and mid-depth during the full deployment to detect vertical shear in the upper layers. At each site, the near-surface and deeper instruments were placed on separate moorings in order to minimize the influence of surface wave action on the deep current measurements. But comparisons between paired VACM and Aanderaa current meters deployed at 15 m during the Cape Sable Experiment indicate that Aanderaa speeds are augmented by only 0.01 $m \cdot s^{-1}$ on average, with direction differences of $\pm 10°$ except during periods of weak currents (Smith et al. 1984).

To protect the instrument moorings from intense fishing (and research) activities in the area, each was placed within a triangular array of guard buoys consisting of 1.3-m steel spheres with mast carrying a light and radar reflector. However, phys-

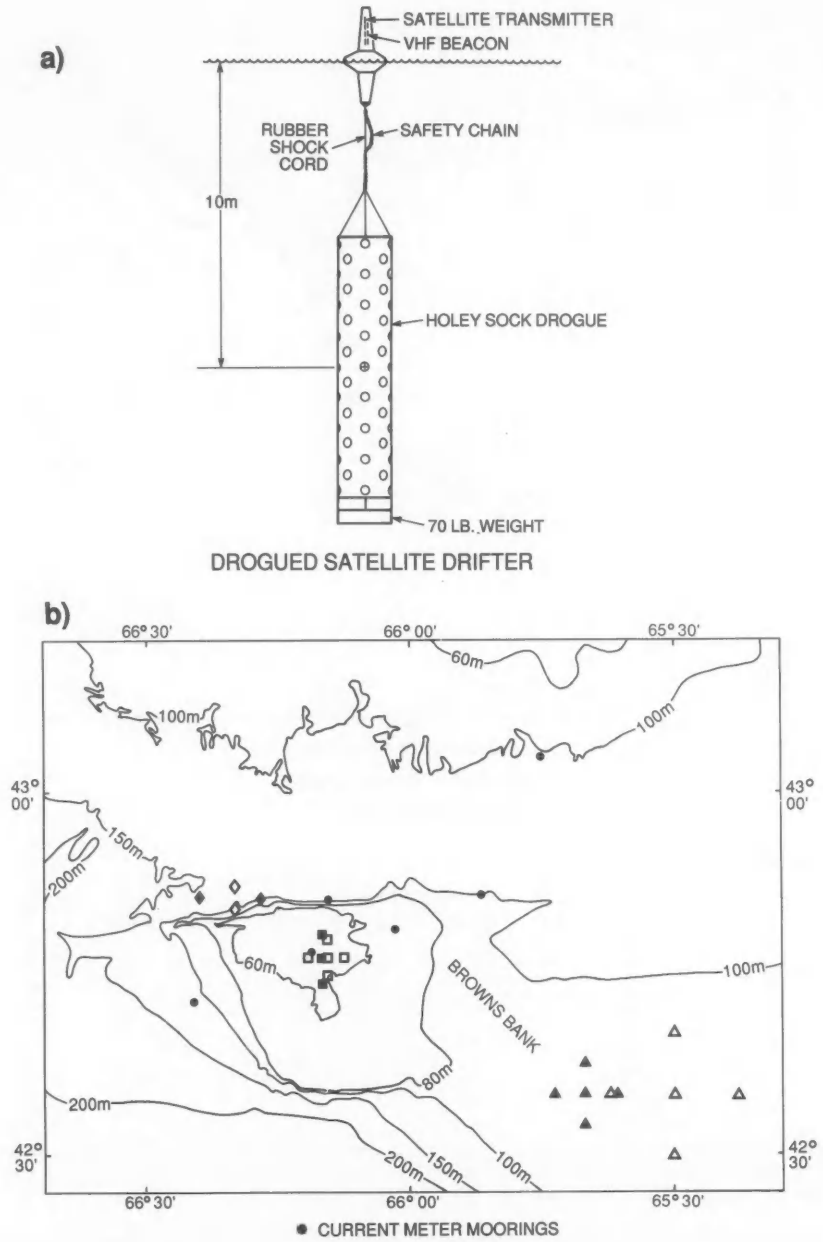

FIG. 2. (a) Schematic diagram of satellite-tracked drifter with "holey sock" drogue centred at 10 m. (b) Deployment arrays for drogue cluster studies during Browns Bank Experiment. Current meter mooring positions are also shown.

ical damage (e.g. lost rotors) caused by strong currents and various electronic failures limited the data return for current measurements to 85%.

In addition to the moored measurements, extensive hydrographic surveys were conducted during the five primary cruises to the area. Accuracies of the standard Guildline digital CTD were typically found to be better than ± 0.01°C and ± 0.01 for temperature and salinity, respectively based on shipboard cal-

TABLE 1. Deployment histories for Browns Bank dispersion studies

Period / ARGOS Buoy ID	Deployment Time	Day	N. Lat.	W. Long.	Recovery Time	Day	N. Lat.	W. Long.	Drogue Type[a]	Comments
April 1983										
2470	0256	97	42°46′	66°10′	1630	99	42°56′	66°25′	WS10	
	1834	100	42°44′	66°02′	0928	107	43°01′	67°11′		
3260	0232	97	42°48′	66°10′	0530	107	43°30′	66°47′	HS10	
3261	0326	97	42°44′	66°10′	0430	107	43°27′	66°51′	HS10	
July/September 1983										
2470	2153	195	42°46′	66°10′	1321	201	43°27′	65°40′	WS30	missing data day 217–219
	2050	207	42°46′	66°10′	1007	228	43°05′	65°39′		
	1340	228	42°44′	66°09′	2202	246	42°59′	66°01′		
2471	2154	195	42°48′	66°10′	1844	209	43°09′	66°29′	WS10	missing data day 217–219
	0732	216	42°49′	66°14′	1921	239	43°04′	65°53′		
2472	0113	196	42°41′	66°10′	1916	198	42°48′	66°20′	WS10	missing data day 217–219
	1142	205	42°47′	66°11′	1402	227	43°32′	67°41′		
	1339	228	42°44′	66°08′	1703	242	43°02′	65°57′		
3260	0113	196	42°43′	66°13′	1832	210	43°15′	66°34′	HS10	missing data day 217–219
	2310	210	42°44′	66°13′	2139	247	44°09′	66°32′		
3261	0114	196	42°44′	66°09′	0955	196	42°50′	66°16′	HS10	missing data day 217–219
	2050	207	42°45′	66°08′	2031	225	43°43′	66°33′		
	0851	226	42°44′	66°07′	1617	246	43°22′	66°28′		
November 1983										
2470	2259	307	42°51′	66°17′	0530	310	43°32′	66°47′	WS10	
	0202	311	42°52′	66°20′	0933	313	42°40′	66°00′		
2472	0130	307	42°51′	66°24′	0111	310	43°13′	66°34′	WS10	
	0220	311	42°50′	66°20′	1458	313	42°43′	66°22′		
May 1984										
2470	1928	124	42°35′	65°23′	1543	144	43°09′	65°37′	HS10	
	0729	146	42°30′	66°01′	0053	149	42°37′	65°49′		
2472	1857	124	42°35′	65°30′	1233	149	43°54′	63°52′	HS10	drogue last day 140
2485	1819	124	42°30′	65°30′	0718	140	43°14′	65°37′	HS10	positions and times approximate
	0652	142	42°40′	65°32′	0222	146	42°56′	65°25′		
	1008	146	42°37′	66°00′	2305	148	42°39′	65°47′		
3260	2018	124	42°40′	65°30′	0320	143	42°35′	67°11′	HS10	positions and times approximate
	0757	144	42°42′	65°34′	0115	146	42°54′	65°36′		
	0529	146	42°32′	65°55′	0229	149	42°36′	65°50′		
3265	2058	124	42°37′	65°37′	0145	145	43°00′	65°34′	HS10	
	0827	146	42°33′	66°01′	0211	149	42°36′	65°51′		
May 1985										
2470	0427	144	42°38′	65°40′	1645	148	42°42′	65°15′	HS10	
2472	0703	144	42°35′	65°37′	1529	148	42°43′	65°22′	HS10	
2485	0638	144	42°33′	65°40′	1243	148	42°44′	65°33′	HS10	
5440	0734	144	42°35′	65°44′	1434	148	42°45′	65°22′	HS10	
5441	0615	144	42°35′	65°40′	1420	148	42°44′	65°22′	HS10	
5442	0612	144	42°35′	65°40′	1426	148	42°45′	65°22′	HS10	redundant central buoy

[a]Drogue type-depth, e.g. HS10 means holey sock drogue at 10 m; WS = window shade.

ibrations against bottle samples and reversing thermometers. Typically, two or three sections were run across the Bank from the coast to the shelfbreak or across Northeast Channel to Georges Bank.

To study localized surface-layer dispersion rates on the Bank, selected regions of the Bank were seeded with clusters of satellite-tracked drifters. Most of the drifters carried "holey sock" drogues centered at a depth of 10 m (Fig. 2a), but no qualitative differences were detected between their performance and that of an earlier version with "window shade" drogues. Initial scales for the drogue clusters ranged between 5 and 20 km (Fig. 2b) and their deployment histories are summarized in Table 1. Relative accuracy of the ARGOS positioning system for these buoys is estimated at ±200 m (D.J. Lawrence, P.O. Box 1006, Dartmouth, N.S. B2Y 4A2, pers. comm.).

With the exception of the July/September 1983 period, the dispersion studies were conducted from a research vessel which was used to supplement the satellite positions with visual sightings and to collect local wind and current information from a bow-mounted anemometer and hull-mounted doppler acoustic current profiler. Wind records were also collected from coastal stations at Yarmouth, Halifax, and Sable Island. During the July/September 1983 period, on the other hand, the drifters were initially deployed by a research vessel on a biological cruise then monitored from shore in near real time via ARGOS. As the buoys exited the Bank region (i.e. beyond 15 km from the

TABLE 2. Record-mean currents and standard deviations from Browns Bank Experiment.

Site (depth)	N. Lat W. Long.	Instrument depth (m)	Start/Stop (DMV)	Duration (d)	V-Axis orientation (°T)	U (m·s^{-1})			V (m·s^{-1})		
						Mean (±SE[a])	σ_1[b]	σ_6[c]	Mean (±SE[a])	σ_1[b]	σ_6[c]
C2	43°02.9′	16	8·4·83/15·9·83	160	104	0.041±0.010	0.121	0.064	−0.007±0.015	0.418	0.083
(110 m)	65°45.5′	15	9·11·83//23·5·84	196		0.012±0.011	0.152	0.093	−0.067±0.027	0.481	0.157
		10	26·5·84/25·11·84	183		0.011±0.013	0.152	0.082	−0.010±0.014	0.439	0.090
		13	25·11·84/24·5·85	180		0.025±0.011	0.156	0.098	−0.060±0.020	0.478	0.124
		50	8·4·83/9·11·83	215	104	0.053±0.007	0.136	0.048	−0.044±0.009	0.471	0.062
		52	9·11·83/23·5·84	196		0.025±0.009	0.116	0.061	−0.076±0.012	0.434	0.100
		50	26·5·84/25·11·84	183		0.038±0.007	0.111	0.045	−0.042±0.008	0.456	0.057
		51	25·11·84/24·5·85	180		0.014±0.008	0.095	0.048	−0.090±0.015	0.444	0.096
		100	8·4·83/9·11·83	215	104	−0.031±0.004	0.115	0.035	0.005±0.005	0.334	0.035
		102	9·11·83/23·5·84	196		−0.009±0.006	0.124	0.054	0.000±0.004	0.294	0.053
		100	26·5·84/25·11·84	183		−0.024±0.006	0.133	0.036	0.025±0.003	0.317	0.035
		101	25·11·84/24·5·85	180		0.011±0.008	0.139	0.061	0.015±0.007	0.327	0.057
C3	42°51.5′	15	8·4·83/6·11·83	212	104	0.051±0.015	0.175	0.087	0.080±0.015	0.417	0.091
(110 m)	65°51.5′	6	6·11·83/16·3·84	130		0.021±0.016	0.228	0.138	0.140±0.028	0.462	0.166
		27	6·11·83/25·5·84	201	104	0.043±0.011	0.218	0.099	0.103±0.023	0.453	0.150
		50	8·4·83/6·11·83	212	104	0.030±0.009	0.154	0.060	0.117±0.006	0.442	0.059
		47	6·11·83/25·5·84	201		0.043±0.010	0.206	0.087	0.127±0.014	0.454	0.130
		100	8·4·83/16·4·83	8	104	−0.052±—	0.178	0.052	0.029±—	0.339	0.078
		97	6·11·83/25·5·84	201		−0.094±0.011	0.214	0.071	0.067±0.008	0.319	0.087
C7	42°50.9′	22	4·11·83/25·5·84	203	90	0.058±0.008	0.282	0.100	0.224±0.022	0.503	0.148
(115 m)	66°09.3′	35	6·12·83/25·5·84	171	90	0.067±0.008	0.277	0.088	0.212±0.015	0.447	0.122
		55	4·11·83/25·5·84	203	90	0.017±0.006	0.246	0.077	0.179±0.011	0.406	0.121
		105	4·11·83/25·5·84	203	90	−0.117±0.006	0.282	0.069	0.148±0.013	0.266	0.101
C8	42°42.3′	16	8·11·83/19·2·84	103	330	−0.027±0.017	0.244	0.102	0.124±0.021	0.501	0.135
(115 m)	66°24.9′	30	8·11·83/24·5·84	198	330	−0.011±0.008	0.192	0.072	0.173±0.022	0.465	0.128
		100	8·11·83/24·5·84	198	330	−0.032±0.009	0.119	0.052	0.044±0.008	0.327	0.065
C9	42°46.4′	14	7·4·83/3·7·83	87	180	0.016±0.011	0.446	0.051	−0.048±0.013	0.431	0.056
(53 m)	66°11.1′	13	3·11·83/8·12·83	35		−0.021±0.036	0.492	0.130	−0.077±0.033	0.461	0.166
		39	7·4·83/3·11·83	210	180	0.045±0.004	0.398	0.047	−0.008±0.006	0.328	0.040
		38	3·11·83/15·3·84	133		0.028±0.010	0.397	0.089	−0.016±0.007	0.360	0.083
C10	42°48.4′	16	6·11·83/24·5·84	200	114	−0.005±0.009	0.292	0.124	0.100±0.017	0.597	0.179
(71 m)	66°01.9′	14	23·6·84/16·11·84	146		0.034±0.009	0.285	0.084	0.120±0.015	0.568	0.106
		15	16·11·84/25·5·85	190		0.026±0.008	0.276	0.107	0.135±0.014	0.558	0.142
		32	7·4·83/6·11·83	213	114	0.046±0.010	0.243	0.054	0.072±0.006	0.502	0.061
		31	6·11·83/24·5·84	200		−0.002±0.006	0.252	0.085	0.078±0.013	0.549	0.141
		28	25·5·84/16·11·84	175		0.027±0.008	0.236	0.054	0.108±0.008	0.559	0.072
		31	16·11·84/25·5·85	190		−0.001±0.005	0.229	0.071	0.109±0.010	0.539	0.114
		61	6·11·83/24·5·84	200	114	−0.003±0.004	0.179	0.058	0.036±0.008	0.395	0.089
		58	25·5·84/16·11·84	175		−0.020±0.006	0.164	0.034	0.060±0.006	0.406	0.058
		61	16·11·84/20·11·84	4		−0.048±—	0.212	0.027	0.082±—	0.379	0.023

[a]σ_1 = Standard deviation for 1-h data.
[b]σ_6 = Standard deviation for low-passed 6-h data (see text).
[c]SE = Standard error of mean = $\sigma_6 n_b^{1/2}$
where n_b = effective number of degrees of freedom (Bayley and Hammersley 1946) is estimated using the integral time scale calculated by integrating under the autocorrelation function for the 6-h data out to the first zero crossing.

100-m isobath), they were retrieved by a Fisheries Patrol Vessel on duty in the area and replaced on the Bank. This technique greatly increased the data return during this quiet summer period.

Results

Mean Circulation and Low-Frequency Variability

The current measurements were resolved into cross-isobath (+ u on-bank) and along-isobath (+ v clockwise) components and filtered to 1-h intervals using a three point running mean (1-h data). For investigating low-frequency phenomena, the records were then low-passed with a Cartwright filter (half-power point at 31-h) and subsampled at 6-h intervals (6-h data).

In winter, the mean currents near the 100-m isobath (Fig. 3a, Table 2) show clear evidence for the existence of a clockwise gyre around the Bank. Through most of the water column, the currents are roughly aligned with the local isobaths with no significant vertical shear. At 10 m above the bottom, however, the measured currents have strong cross-isobath components in the off-bank direction, particularly on the northern flank (C7, C3). The current magnitudes are largest (0.19–0.23 m·s^{-1}) on the northern flank where the bottom slope is a maximum (at C7), diminished somewhat (0.04–0.14 m·s^{-1}) at the 70-m isobath (C10), and generally weak and variable on the cap of

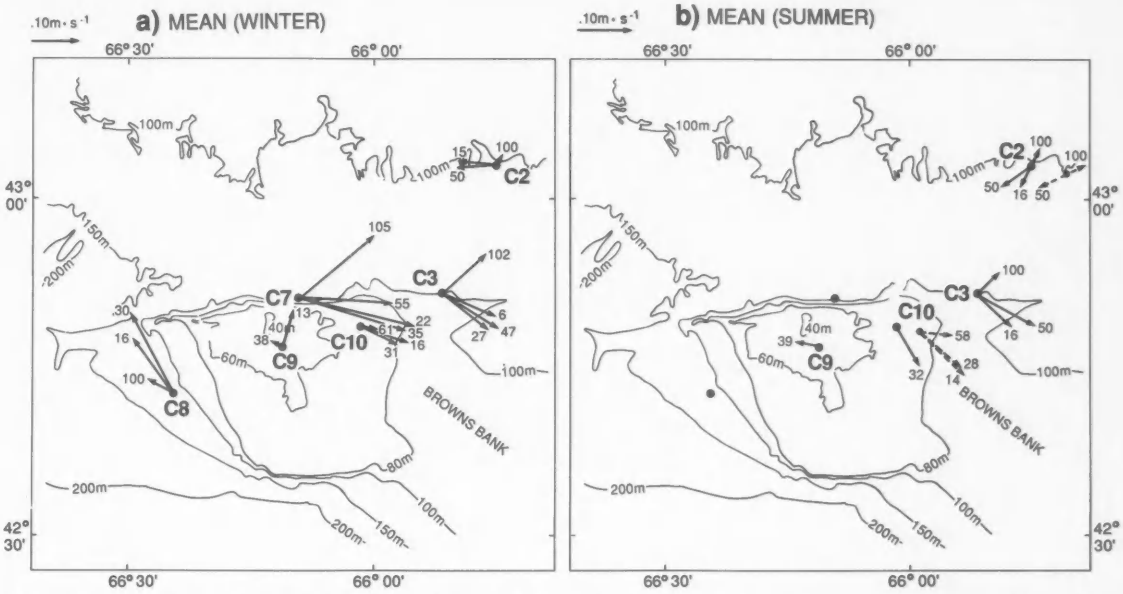

FIG. 3. (a) Mean currents during winter 1983/1984 deployment of Browns Bank moorings. (b) Mean currents during summer 1983 (solid) and summer 1984 (broken) deployments of Browns Bank moorings.

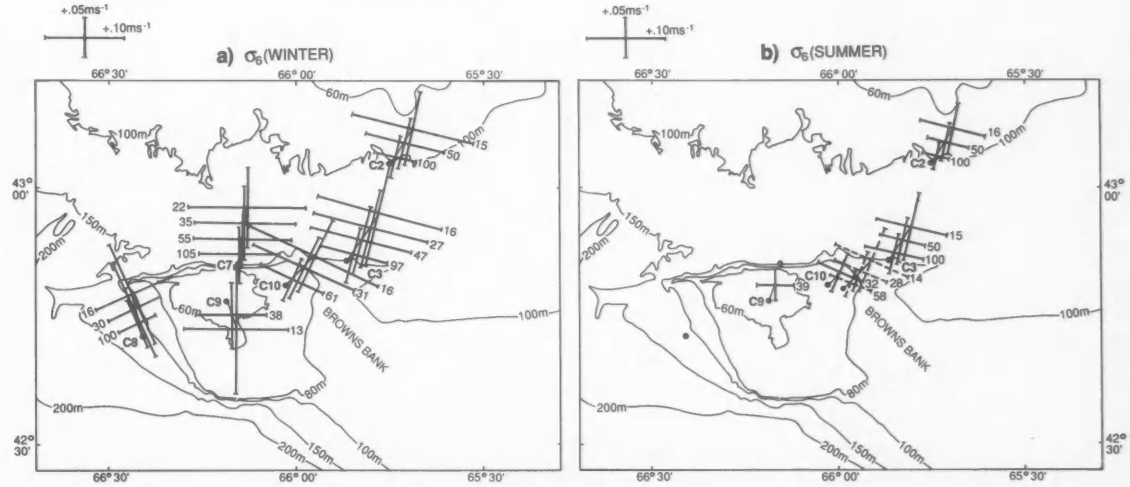

FIG. 4. (a) Low-frequency standard deviations of along- and across-isobath current components during winter 1983/1984. (b) Low-frequency standard deviations of current components during summer 1983 (solid) and summer 1984 (broken).

the Bank (C9). Across the northern channel at C2, the mean currents are weaker than the Bank currents at similar depths and generally directed into the Gulf of Maine along the 100-m isobath. However, the bottom current in the inshore zone is weak and shoreward. The small size of the standard errors (typically less than 10% of the mean; Table 2) indicates that these estimates of the mean circulations are robust.

The summertime currents at C3 and C10 (Fig. 3b; Table 2) are similar in both magnitude and direction to those in winter, which supports the permanent nature of the gyre circulation. At C3 some weak seasonal variations, such as the tendency for surface currents to veer toward shallow water in summer (Table 2), have been noted in the earlier measurements from the Cape Sable Experiment (Smith 1983). However, a strong seasonal signal in the along-isobath component was not found in either the present or previous data. Similarly, the C10 summer mean currents at both surface and mid-depth were rotated toward the centre of the Bank with respect to their wintertime orientations. Bottom currents at both sites were oriented down slope with respect to the flow above. In the inshore zone, the C2 surface and mid-depth currents appear to be deflected offshore in summer while the onshore bottom flow is intensified.

The low-frequency variability in the current field over Browns Bank, characterized by the standard deviation of the 6-h data (σ_6; see Table 2), typically exceeds the mean current magnitude in winter but shows a distinct seasonal variation

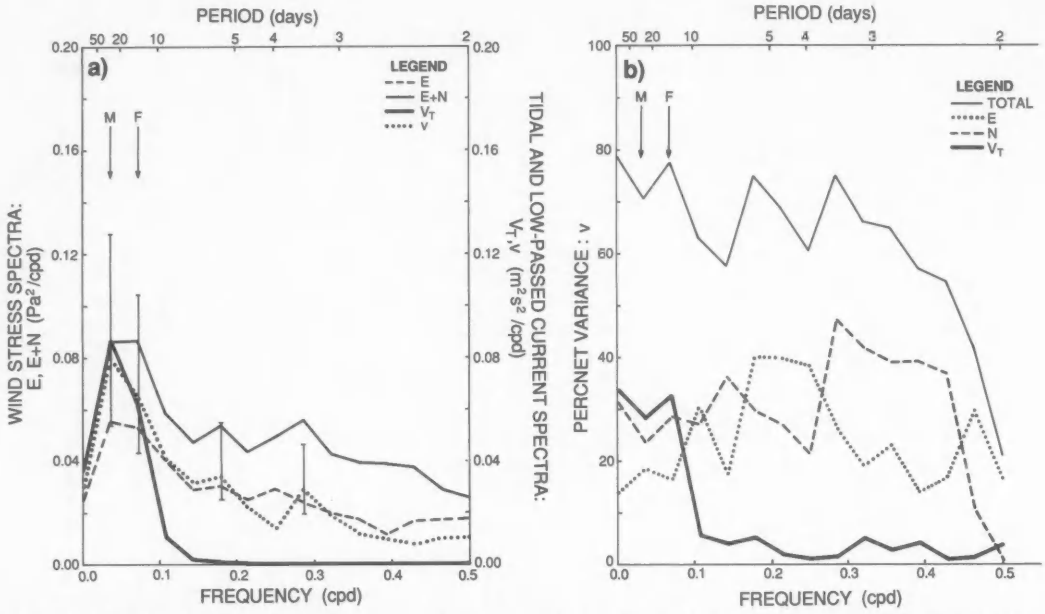

FIG. 5. (a) Autospectra for along-isobath (104°*T*) component of low-passed current, *v* at C3 (15 m); major-axis amplitude of tidal current, V_T; and east, *E*, and north, *N*, components of sea surface wind stress at Sable Island. Spectra are calculated for year-long records from August 1979 to August 1980. Monthly (*M*, 28 d) and fortnightly (*F*, 14 d) spectral bands are indicated. Error bars represent 95% confidence limits on *v* based on 41 degrees of freedom. (b) Relative contributions to the total current variance from tidal, V_T, and wind (*E*,*N*) forcings.

(Fig. 4a, b). The largest values of σ_6 are found near the surface and diminish rather uniformly with depth to a near-bottom value roughly half that at the surface. The variance is essentially isotropic over the shallow cap, but tends to be weakly anisotropic in favour of the along-isobath component over the flanks of the Bank, especially near the bottom (Fig. 4a). The high level of energy in the subtidal current field means that daily average currents on the Bank can be significantly different from the seasonal mean values. Furthermore, tidal currents are the dominant factor in determining the total current variance as may be seen by comparing the 1-h and 6-h standard deviations (σ_1 and σ_6).

Wind and Tidal Forcing at Low-Frequencies

In the waters off Southwest Nova Scotia, low-frequency current variability with characteristic periods of 2–30 d is forced primarily by wind and nonlinear interactions of the tide. Smith (1983) has demonstrated significant coherence between low-passed current components and the local major axis amplitude (V_T) of the M_2 semidiurnal tidal ellipse. Furthermore, using a frequency-dependent multiple regression technique (Garrett and Toulany (1982)), Tee et al. (1987, 1988) have recently analyzed records longer than 1 yr to separate the effects of tidal and two components of wind stress forcing on low-frequency currents. For tidal forcing, significant responses were found in the monthly (≈28 d) and fortnightly (≈14 d) spectral bands at selected sites including C3. A comparison of the autospectra of the along-isobath (104°*T*) current component at C3 (15 m) to those of tidal (V_T) and Sable Island wind stress (*E* = east, *N* = north) forcings (Fig. 5a) reveals that a substantial fraction of the subtidal current variance is found in bands centered on the monthly and fortnightly frequencies, which also contain virtually all of the tidal and a large part of the wind stress variability. Note that the absence of significant tidal forcing from the higher frequency bands is contrary to Magnell et al.'s (1980) observations of tidal current modulations at wind-driven time scales of 3–5 d on the northern flank of Georges Bank. The presence of strong wind forcing at periods longer than those of the synoptic atmospheric forcing (2–10 d periods) is also surprising. Figure 5b demonstrates that tidal and wind forcings make roughly equal contributions to the total near-surface current variance in the monthly and fortnightly bands, whereas wind stress components alone contribute 30–40% each in the synoptic bands. Overall the regression accounts for 70–80% of the variance at periods longer than 10 d and 60–70% between 2.5 and 10 d. Analysis of shorter near-bottom records at C3 reveals some coherent modulations in the cross-isobath current and tidal forcing, but statistical confidence in this connection is weaker than at C3 (15 m). A more complete analysis of these results and others from the Cape Sable/Browns Bank area is in preparation.

Although the relationship between low-frequency modulations of tidal amplitude and current seems clear, it is not yet possible to define unambiguously the component of the residual circulation which is tidally-driven (Tee et al. 1988). The problem is related to uncertainty in the (presumed) power law dependence (ϵ) of the residual current vector (u_2) on the tidal forcing (V_T = semi-major axis of tidal current ellipse) in the statistical model formula:

$$u_2 = aV_T^{\epsilon} + bE + cN + noise,$$

where (*a*, *b*, *c*) are vector coefficients and *E* and *N* are the local east and north components of sea surface wind stress. With this simple power law dependence, it is clear that the value of ϵ must be known accurately in order to determine the mean tid-

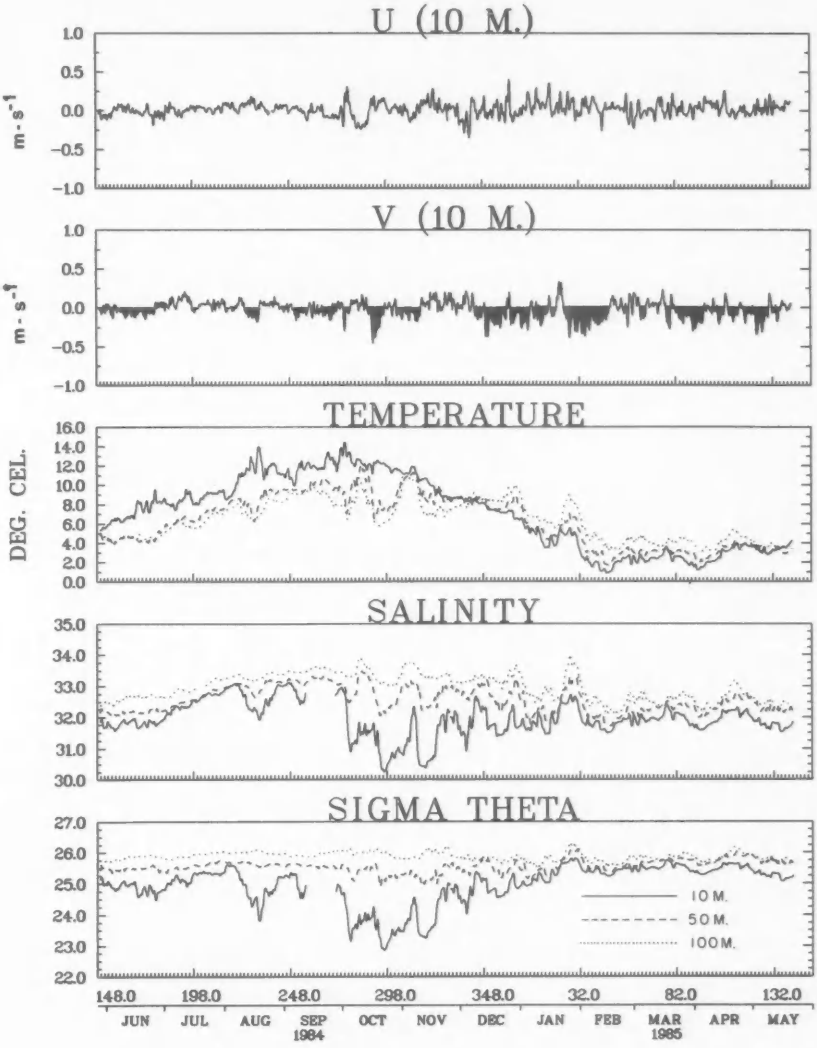

FIG. 6. Year-long records (May 1984–May 1985) of low-frequency current components, u (194°T) and v (104°T); temperature, T; salinity, S; and density anomaly, σ_θ, from the C2 mooring off Cape Sable. Periods of negative along-isobath surface current (i.e. into the Gulf of Maine) are emphasized by solid shading and records of hydrographic properties from three depths are shown.

ally-induced current. However, a 3-D numerical model suggests that ϵ varies widely ($0 \leq \epsilon \leq 3$) in the Cape Sable/Browns Bank area due to the complicated structure of tidally-induced pressure gradients and nonlinear interactions. Furthermore, attempts to validate numerical model results with observations are frustrated by the inability of the model to resolve adequately the bathymetric structure of the Bank (see Tee et al. 1988, for more detail). Thus quantitative theoretical confirmation of the magnitude of the tidal residual circulation is not achievable at present.

Hydrographic Observations

Previous moored and hydrographic measurements from this region (Smith 1983) indicate that the normal seasonal progression from stratified summer to unstratified winter conditions is interrupted by the arrival of a succession of low salinity pulses carried down the Scotian Shelf by coastal currents. The most dramatic effects are associated with large pulses which appear first in the inshore zone in late autumn and are thought to originate in the Gulf of St. Lawrence. Year-long records from C2 (Fig. 6) reveal that in 1984, the major pulses arrived somewhat early (near the beginning of October) and were preceeded by weaker anomalies which first appeared in early August. The earlier temperature anomalies are warm near the surface and cold at depth. However, the salinity anomalies, which control the density, are negative throughout the water column. The

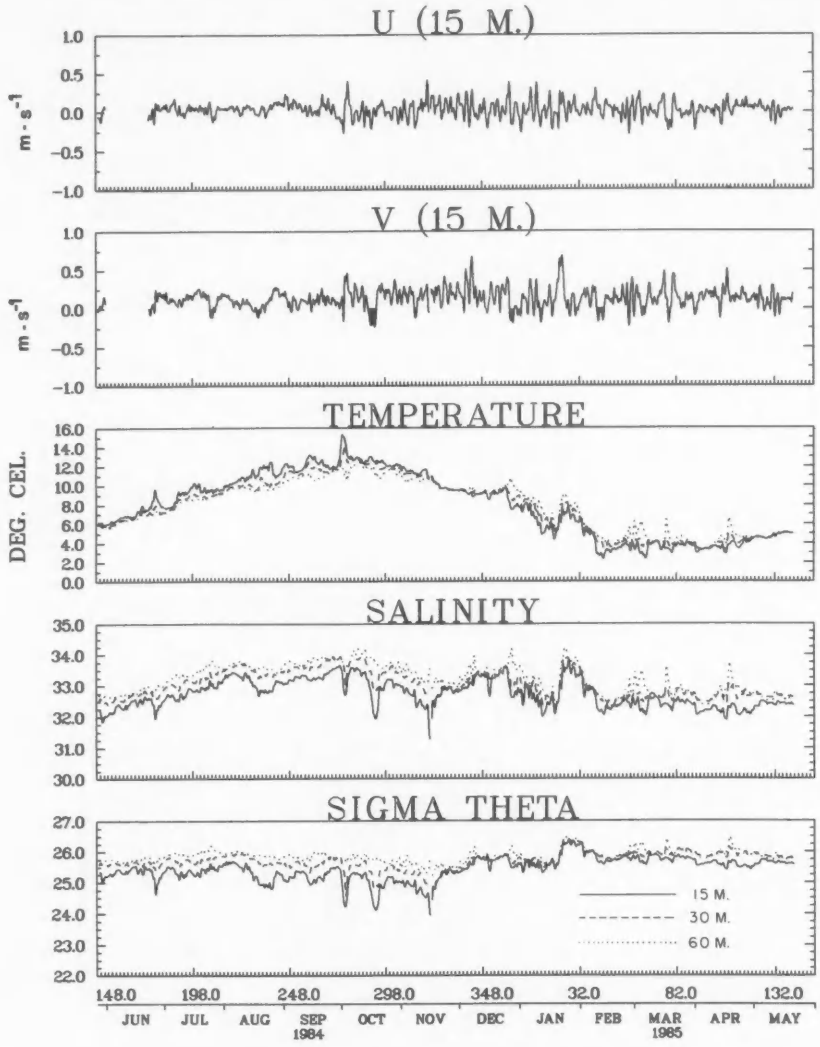

FIG. 7. Year-long (May 1984–May 1985) record of low-frequency current components, u (204°T) and v (114°T); temperature, T; salinity, S; and density anomaly, σ_θ, from the C10 mooring on Browns Bank. Periods of negative along-isobath surface current are emphasized and hydrographic properties at three depths are shown. Apparent jumps in S and σ_θ at breaks in records represent small (<0.1) calibration errors in the conductivity cells.

splaying of σ_θ contours as the pulses arrive indicates a sharp increase in stratification. At site C10 on the Bank (Fig. 7), some of the same pulses are detected in the salinity records, but their effects do not persist as long as at C2. Qualitatively similar observations can be made about the records from 1983, but the failure of the conductivity cells makes quantitative assessment of the anomalies difficult. Interannual variability of the strength and timing of the low salinity pulses from 6 yr of observations at C2 is presently under investigation.

The hydrographic sections from early November 1983 (Fig. 8a–c), reveal the influence of the low salinity pulses on the northern side of the Bank. Fresh light surface water occupies the top 50 m of the water column, and even at depths of 100 m or more, there is a salinity difference of greater than one unit across the Bank. This suggests that warm slope water is intruding into the Gulf of Maine through Northeast Channel at the same time as the low salinity water is arriving off Cape Sable. The buoyancy fluxes associated with these flows are evidently responsible for maintaining the stratification of the deeper regions; however the water over the shallow cap appears to be well-mixed. This conclusion is confirmed by comparing density (σ_θ) profiles near the 100-m isobath with one from the cap (Fig. 8d). The presence of this mixed water over the shallow regions of the cap is qualitatively consistent with the recent

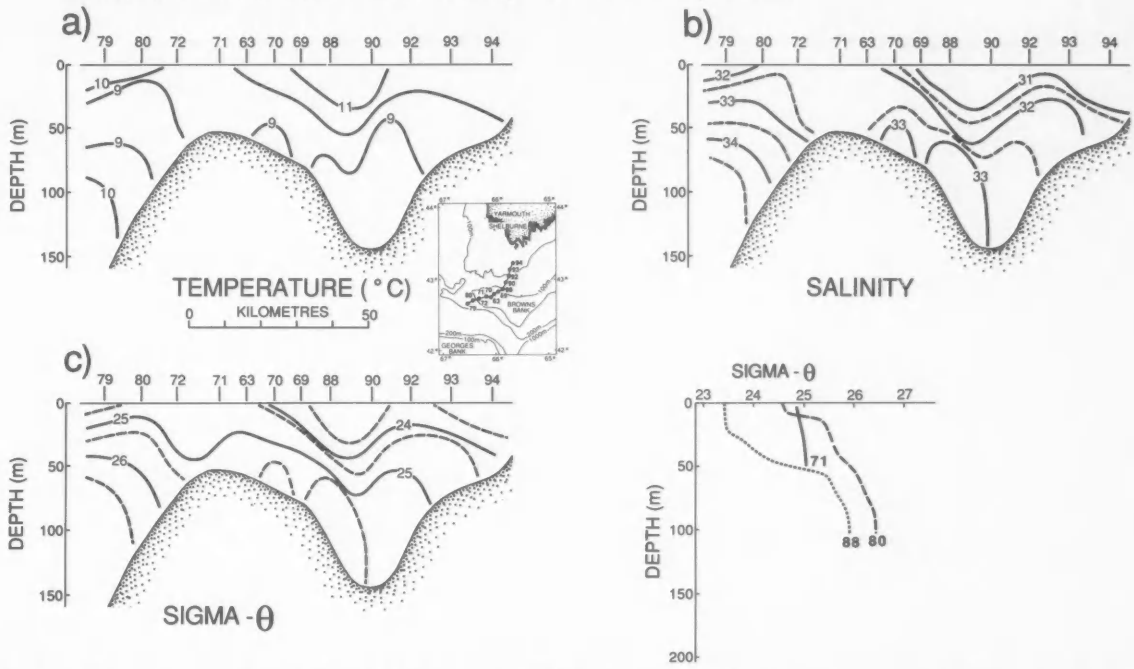

FIG. 8. Hydrographic sections from Cape Sable across Browns Bank during November 2–10, 1983. (a) Temperature (°C) (b) Salinity (c) Sigma-θ. Also shown are (d) sigma-θ profiles from stations on the cap (71), northern (88), and western (80) flanks of the Bank.

results of Loder and Greenberg (1986), who concluded that tidal mixing on the cap was sufficient to overcome the stratifying influence of solar insolation. In this season, however, the net surface heat flux is near zero and the tidal mixing must counteract the buoyancy inputs associated with horizontal advection of Scotian Shelf water and offshore slope water. On the northern flank near C3 (i.e. Stn. 88), the thermal wind relation implies a negative vertical shear (0–50 m) in the clockwise current around the Bank of approximately $-0.15\ \mathrm{m \cdot s^{-1}}$, which compares favorably to the average measured shear (15–50 m) of $-0.20\ \mathrm{m \cdot s^{-1}}$ during the passage of the pulse. However, the overall effect of these events on the seasonal mean shear is small (Fig. 3).

A similar section from April 1983 (Fig. 9a–c) shows higher salinities inshore and a smaller salinity contrast across the Bank. Again however, the water on the cap is less stratified than that over the flanks, but the horizontal density gradients (and inferred geostrophic shear) are considerably reduced.

Lagrangian Drift Tracks

To focus on the net displacement of the buoys, trajectories were smoothed by interpolating the positions in time to the start of each day. Based on an average interpolation interval of 2 h, this introduces an uncertainty of 1 km in the indicated positions.

The drift tracks for individual buoys deployed as clusters during the mooring cruises show a fair degree of similarity (Fig. 10) but can be quite different from those of the same buoys deployed at roughly the same locations at different times. For example, three identical drifters released at 2-nm (3.7 km) intervals on the western cap in April 1983, followed essentially the same paths, leaving the Bank to the north and moving into the Gulf of Maine (Fig. 10a). However, the tracks of two buoys deployed twice within 4 d on the northern flank in November 1983 (Fig. 10b, c), showed marked differences between deployments. Similarly, separate deployments of 5- and 6-drogue clusters in the saddle region of the Bank during the haddock spawning season (May 1984 and 1985; Fig. 10d–f) resulted in qualitatively different behaviour. In 1984 all buoys were advected westward around the cap and then left the Bank, whereas in 1985 the observed drift was slower and more steadily to the northeast. These differences again indicate the rich spectrum of temporal variability in the current regime.

Selected portions of the drift tracks for buoys deployed on the cap of the Bank during the summer period, July/September 1983, are reasonably consistent with the gyre circulation (Fig. 11). A typical circuit around the western cap of the Bank between the 80- and 120-m isobaths would require 12 d (Table 3; Fig. 11b); however, most buoys depart from the Bank to the north before completing a full loop. In addition, some buoys appear to be trapped in the central cap region for several days before spiralling outward to leave the Bank (e.g. Fig. 11c, d). In order to quantify the observed residence time during this period, the total number of days each undisturbed (e.g. by fishermen) buoy remained on the Bank or within 15 km of the 100-m isobath has been computed (Table 3). The exit criterion (15 km from 100-m isobath) is representative of both (1) the maximum tidal excursion on the Bank, and (2) the distance between the 100 m isobath on the northern flank and latitude 43°N, which the drift tracks suggest is the outer boundary of the inshore current flowing into the Gulf of Maine. According to this criterion, the longest residence times are of order 25 d, whereas

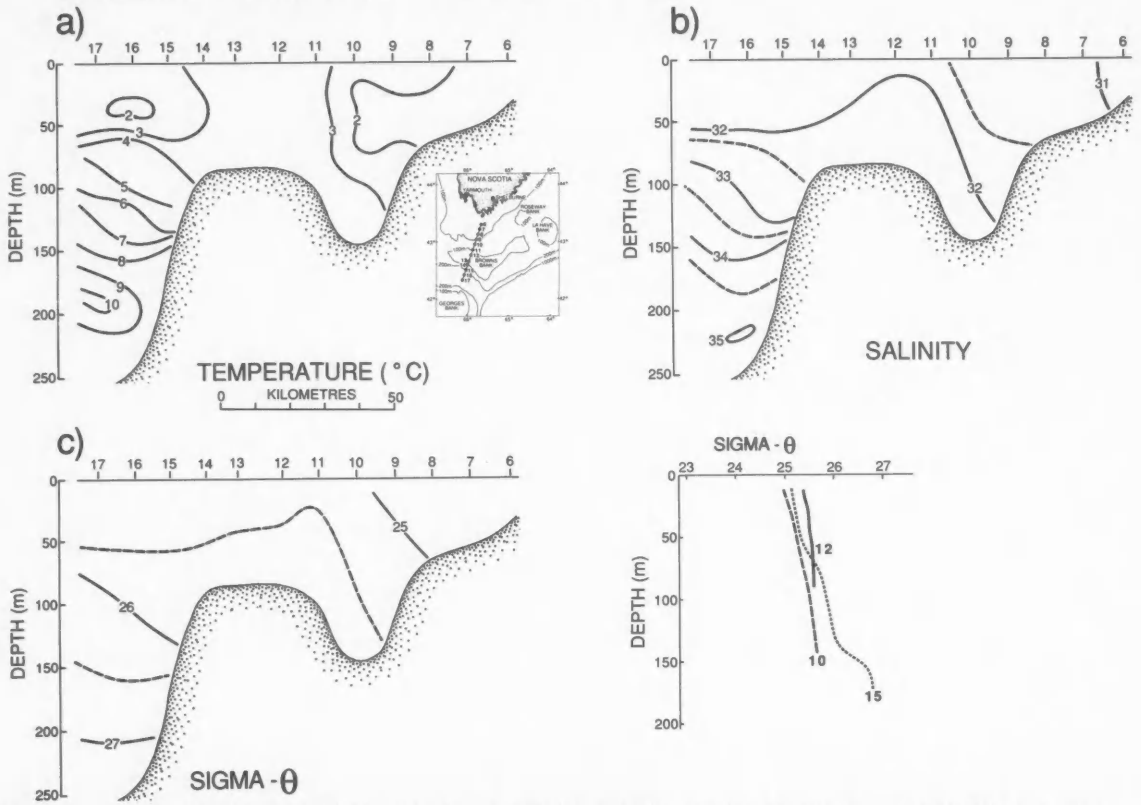

FIG. 9. Hydrographic sections from Cape Sable across Browns Bank during April 5–12, 1983. (a) Temperature (°C) (b) Salinity (c) Sigma-θ. Also shown are (d) sigma-θ profiles from stations on the cap (12), northern (10) and southern (15) flanks of the Bank.

minimum times are of order 5 d. Over the 10 separate deployments, the average duration on the Bank was 14.3 d.

Effects of Wind on Buoy Trajectories

A possible clue to the difference between the trajectories of identical buoys launched in the same location at different times comes from examination of measured winds at nearby coastal stations. For example, Sable Island winds (Fig. 12) during the two successive deployments on the northern flank in November 1983 (Fig. 10b, c), indicate a prevailing westward wind (to the west) during the first deployment and eastward wind during the second. Wright et al. (1986) have demonstrated that (1) the steady response to alongshore wind (56°*T*) is generally much stronger than that to the cross-shore component (146°*T*), (2) Sable Island wind is a reasonable proxy for low-frequency atmospheric forcing over the Gulf of Maine and Scotian Shelf, and (3) the current response to alongshore wind is relatively uniform over Browns Bank and the inshore zone off Cape Sable (Wright et al., Fig. 4 and 8). Therefore, assuming that the measured low-frequency response at C3 (15 m) is representative of the wind-driven component of the current at drogue depth (10 m) over the entire region of interest (and neglecting both Stoke's drift and slippage caused by wind waves and current shear), it is possible to estimate the wind-driven component of the observed drift velocity as,

$$(1a)\quad U_W = G_{XU}X + G_{YU}Y$$

$$(1b)\quad V_W = G_{XV}X + G_{YV}Y$$

where (X,Y) are the across- and along-shore components of sea surface wind stress calculated according to the formulae of Smith and Banke (1975) and $(G_X, G_Y)_{U,V}$ are the observed current gains with respect to that forcing, derived from the multiple regression analysis at zero frequency. Although the winds are variable, this approximation is valid because the response curves are nearly flat down to periods of at least 4 d.

The wind-driven currents estimated from daily average wind stress in this manner are indicated in Fig. 10a–c for the April and November 1983 deployments. Apparently, though the wind-driven component does not account for the full Lagrangian trajectory, it may be sufficient to "kick" the drifter out of the gyre and into another regime. This process would also depend, to some extent, on the difference in the stage of the tide when the drogues were deployed. However, the major axis of the M_2 tidal ellipse in this region (10 km) is smaller than the net displacements due to wind.

Differential Kinematic Properties and Dispersion Rates

A least-squares technique for determining the 2-D differential kinematic properties of oceanic flow fields from the motion

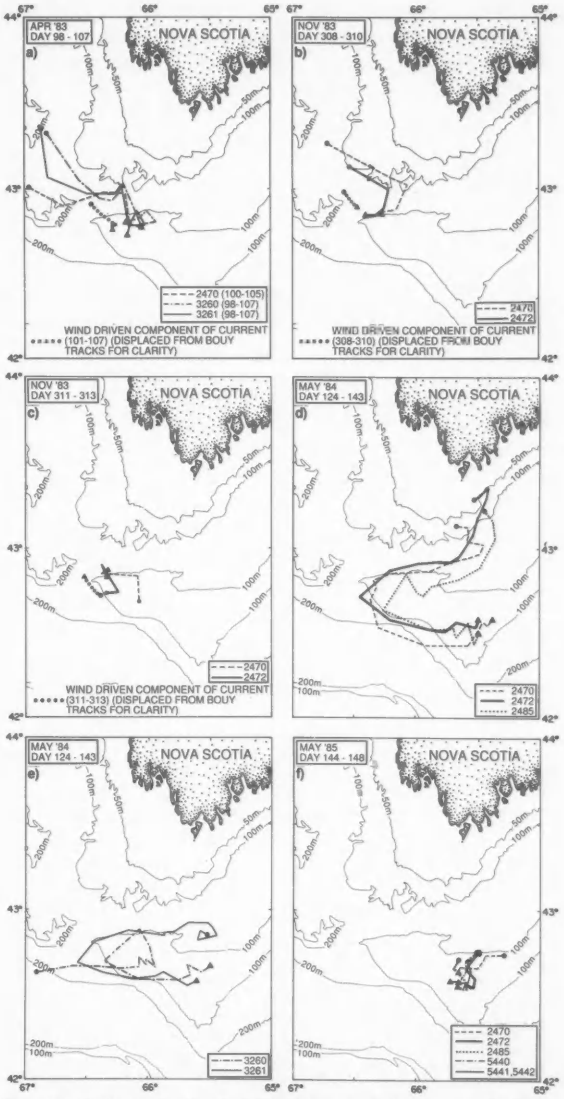

FIG. 10. Drift tracks for individual buoys during seasonal cluster experiments. A triangle and a solid circle mark the beginning and end of each track, respectively. (a) April 1983; days 98–107, (b) November 1983; days 308–310, (c) November 1983; days 311–313, (d) May 1984; days 125–143, (e) May 1984; days 125–143, (f) May 1985; days 144–148. Also shown on (a)–(c) is the estimated wind drift (dotted curve, offset for clarity) calculated from the measured steady wind-driven response at C3 (15 m) over the period of deployment (see text).

of clusters of Lagrangian drifters has been described by Okubo and Ebbesmeyer (1976). The method involves expansion of the horizontal velocity components of n drogues, observed at time $t=t_k$, in Taylor series about the centroid of the cluster, i.e.

$$(2a)\quad u_i(t_k) = \bar{u} + \frac{\partial u}{\partial x} x_i + \frac{\partial u}{\partial y} y_i + y_i''$$

$$(i=1,..n;\ k=1,..m)$$

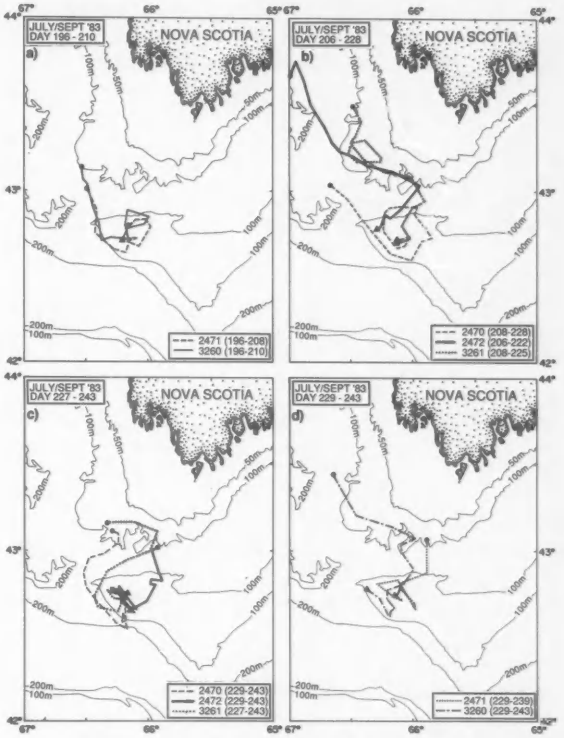

FIG. 11. Drift tracks as described in Fig. 10 but for July/August, 1983. (a) days 196–210, (b) days 206–228, (c) days 229–243, (d) days 229–243 (These tracks represent portions of longer buoy trajectories).

$$(2b)\quad v_i(t_k) = \bar{v} + \frac{\partial v}{\partial x} x_i + \frac{\partial v}{\partial y} y_i + v_i'',$$

where $(\bar{u}, \bar{v})$ are the velocity components of the centroid; (x_i, y_i) are the displacements of the drogues relative to the centroid; $(\partial u/\partial x, \partial u/\partial y, \partial v/\partial x, \partial v/\partial y)$ are the velocity gradients along x (east) and y (north); and (u_i'', v_i'') are velocity residuals. For $n \geq 4$, the gradient and mean velocity components may be estimated by minimizing the sums of the square residuals, and then combined to form the differential kinematic properties (DKP):

$$(3a)\quad \Delta(t_k) = \frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} = \text{horizontal divergence}$$

$$(3b)\quad \eta(t_k) = \frac{\partial v}{\partial x} - \frac{\partial u}{\partial y} = \text{relative vorticity}$$

$$(3c)\quad a(t_k) = \frac{\partial v}{\partial x} + \frac{\partial u}{\partial y} = \text{shearing deformation rate}$$

$$(3d)\quad \beta(t_k) = \frac{\partial u}{\partial x} - \frac{\partial v}{\partial y} = \text{stretching deformation rate.}$$

Divergence and vorticity (positive counterclockwise) are invariant under rotation of the coordinate axes, whereas the shear and deformation rates have extrema along principal axes which are offset by 45°(EG & G 1979).

TABLE 3. Observed recirculation and residence times for near-surface drogued drifters on Browns Bank during July/September 1983.

Buoy number	Day deployed[a]	Day of exit[b]	Residence time[b] (d)	Recirculation time[c] (d)	Comment
2471	195	208	13	12	(estimated from partial circuit)
3260	196	207	11	8–11	(estimated from partial circuit)
2470	207	227	20	12	good estimate of recirculation time
2472	205	211	6		no evidence for gyre circulation
3261	207	212	5		no evidence for gyre circulation
2470	228	239	11	12	(estimated from partial circuit)
2472	228	239	14		no evidence for gyre circulation
3261	226	240	14	8	(estimated from partial circuit)
2471	216	239	23		buoy "trapped" on cap; no evidence for gyre
3260	211	237	26		buoy "trapped" on cap; no evidence for gyre
		Average	14 d		

[a]Buoys deployed near 42°46′N, 66°10′W by Fisheries Patrol Vessels (see Table 1).
[b]Exit criterion is displacement of the buoy by more than 15 km outside 100-m isobath, and residence time is defined as the difference between deployment and exit dates.
[c]Recirculation time is estimated by dividing the circumference of the western cap region between the 80- and 120-m isobaths by the average rate at which the buoy travels along some portion of that boundary.

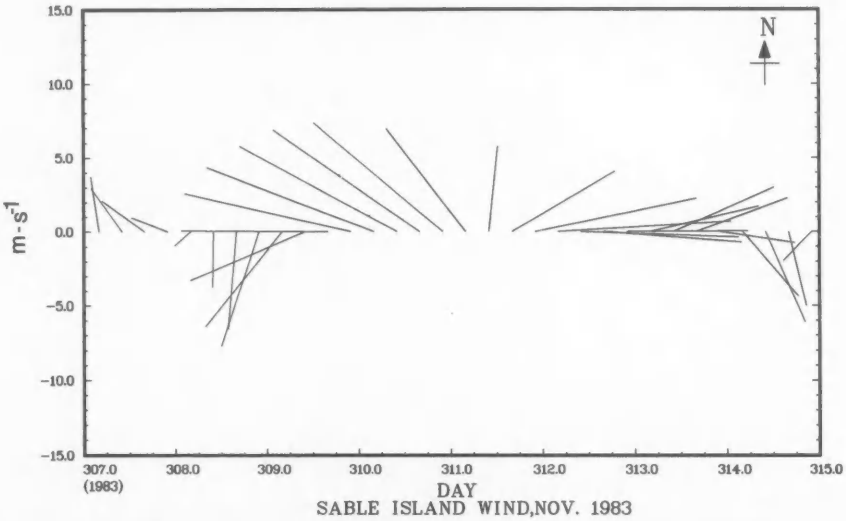

FIG. 12. Stick plot of low-passed 6-h wind vectors at Sable Island during November 1983.

Since the Taylor expansion requires simultaneous estimates of position and velocity for each drogue, the velocity components calculated from the differences between two successive position fixes were associated with the mid-point position of the displacement vector. (More sophisticated techniques such as spline fitting of the position data (Molinari and Kirwan 1975) were rejected because the tidal motion was not fully resolved by the sampling scheme.) Position and velocity errors associated with this procedure are included in the velocity residual terms (u_i'', v_i'') along with measurement errors in the satellite positions, nonlinearities in the velocity gradients, and true turbulence. The influence of satellite position errors on DKP was estimated by comparing the original calculation with a second in which positions were perturbed by random fluctuations in the range of the ARGOS uncertainty (±200 m). The differences between the two DKP estimates was typically less than 20% of the original estimate. However, the statistical errors in the DKP, measured by rms standard errors in the velocity gradients which are calculated in the least squares analysis (Draper and Smith 1966), are found to be of the same order as the DKP themselves. This implies that for the small number of drogues used, the 95% confidence limits on the DKP estimates are typically 3–4 times the estimated value. (Okubo and Ebbesmeyer (1976) suggest that such practical limitations of this method may be overcome by using clusters of six or more drogues, but resources were not sufficient in this case.)

In order to gain some confidence in the reliability of the DKP estimates, time series of vorticity and divergence were used to test the simple vorticity balance,

$$(4)\quad \frac{d\eta}{dt} + f\Delta = 0,$$

where $f(\approx 10^{-4}\cdot s^{-1})$ is the Coriolis parameter. This relation

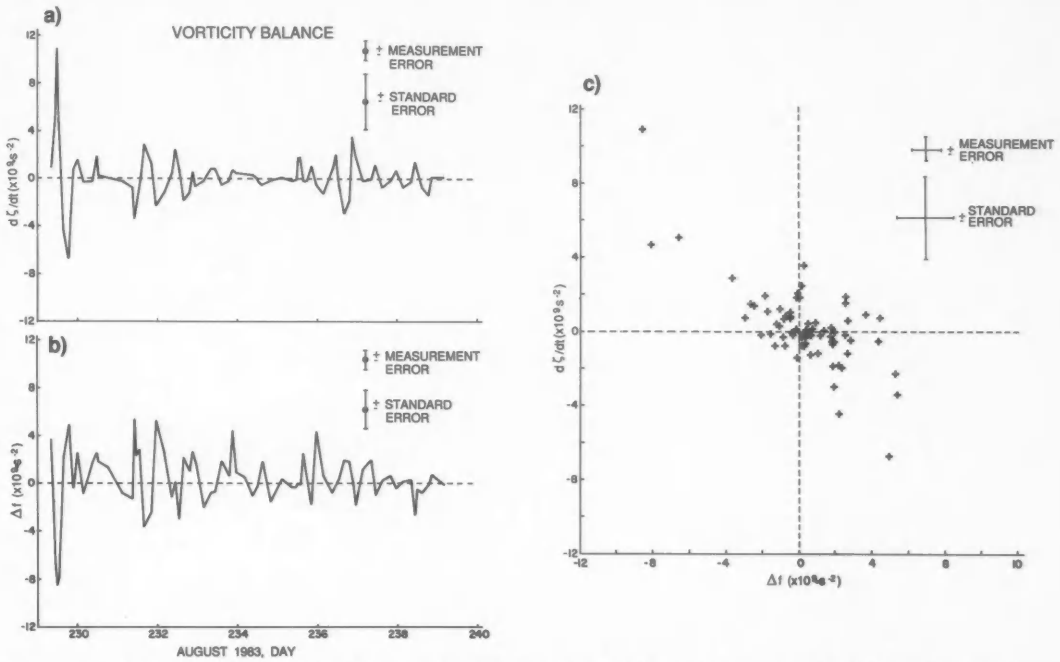

FIG. 13. Time series of terms in simple vorticity balance estimated from differential kinematic properties (DKP) of five-drogue clusters during days 229–239, 1983. Typical measurement errors and standard errors of the DKP terms are shown. (a) rate of change of relative vorticity, (b) Coriolis parameter ($f \approx 10^{-4} \cdot s^{-1}$) times horizontal divergence, (c) scatterplot of (a) versus (b).

TABLE 4. Estimates of the average horizontal eddy diffusivity on Browns Bank.

Period (d)	Number of drogues	Anisotropic ($c = 0.1$) $K_x \pm SD_x$[a] ($m^2 \cdot s^{-1}$)	Anisotropic ($c = 0.1$) $K_y \pm SD_y$[a] ($m^2 \cdot s^{-1}$)	Start ℓ_o[b] (km)	Start K_{HO}[a] ($m^2 \cdot s^{-1}$)	End ℓ_E[b] (km)	End K_{HE}[c] ($m^2 \cdot s^{-1}$)	Regression ℓ_R[b] (km)	Regression K_{HR}[c] ($m^2 \cdot s^{-1}$)	Region of bank
April 1983 (day 100–107)	3	—	—	13	10	71	141	57	95	Western cap/ northern flank/inshore
August 1983 (day 229–239)	5	102 ± 117	68 ± 46	20	17	53	50	58	60	Western cap/northern flank/inshore
May 1984 (day 125–140)	5	127 ± 104	115 ± 126	29	26	113	160	103	122	Saddle/western cap/ inshore
May 1985 (day 144–148)	6	25 ± 27	16 ± 12	16	13	27	23	28	21	Saddle

[a] SD_x, SD_y are the standard deviations of $K_x(t_k)$, $K_y(t_k)$ about mean values.
[b] Cluster scale, see text (8b).
[c] Apparent diffusivity, see text (7).

implies that friction is weak and that there is no significant curl in the external forces, such as surface wind stress. Separate estimates of the two terms in this balance were obtained at the midpoints of the time intervals between DKP calculations using finite differences for the vorticity gradient and a simple mean for the divergence. Time series for the August 1983 period (Fig. 13a, b) reveal that, in spite of the lack of statistical confidence in the DKP, the fluctuations in the two dynamical quantities are of the same order of magnitude and out of phase. Furthermore, a plot $d\eta/dt$ against $f\Delta$ (Fig. 13c) clearly shows the inverse relationship and that deviations from it are of the same order as those associated with the standard errors in the DKP.

Similar results were obtained for the time-dependent vorticity balances in May 1984 and May 1985, however, large errors associated with the small number of drifters (three) in April 1983 precluded such a test. In addition, an attempt was made to relate changes in relative vorticity to those in the average water depth, h, according to the conservation of potential vorticity:

$$(5) \quad \frac{d\eta}{dt} = \frac{f}{\bar{h}} \frac{d\bar{h}}{dt},$$

where $\bar{h}$ is estimated from the ensemble mean of the local water depth at the buoys. However, estimates of the terms in equation (5) could not be balanced, probably because of: (1) poor estimation of changes in the average water depth by $\bar{h}$, and (2) errors in the model which assumes that the current field is uni-

form with depth. A similar conclusion was reached by EG & G (1979).

If the velocity residuals (u'', v'') are assumed to represent primarily turbulence rather than random error, an estimate of the time-dependent anisotropic eddy diffusivity may be obtained by analogy to mixing length theory (Okubo and Ebbesmeyer 1976) as

(6a) $K_x(t_k) = c\sigma_{u''}\sigma_x$,

(6b) $K_y(t_k) = c\sigma_{v''}\sigma_y$,

where

$$(\sigma_{u''}, \sigma_{v''}) = \left[\frac{1}{n-1}\left(\sum_1^n u_i''^2, \sum_1^n v_i''^2\right)\right]^{1/2}$$

and

$$(\sigma_x, \sigma_y) = \left[\frac{1}{n-1}\left(\sum_1^n x_i^2, \sum_1^n y_i^2\right)\right]^{1/2}$$

are the turbulence intensity and mixing length components, respectively. The constant c, thought to be between 0.1 and 1.0 (Okubo and Ebbesmeyer 1976), is chosen to be 0.1 for consistency with other measures of the diffusivity (see below). The average values of K_x, K_y computed over the various deployments of the drogue clusters (Table 4) suggest a moderate spatial variation of the diffusivity with somewhat higher values on the western cap and northern flank than in the saddle. However, the large standard deviations about these means indicates a low level of confidence in this conclusion. Furthermore, no significant anisotropy in the diffusivity can be resolved.

As a basis for comparison with other estimates in the literature, an alternative measure of horizontal dispersion, the apparent diffusivity, K_H (Okubo 1971), may be calculated from the mean square distance of the drogues from the centroid, i.e.

$$(7)\quad K_H = \frac{\sigma_{rc}^2}{4(t+t_0)},$$

where

$$\sigma_{rc}^2 = (1/n)\sum_1^n x_i^2 + y_i^2$$

and $(t+t_0)$ is the diffusion time (seconds). For the cluster experiments, $t=0$ is the time of deployment and t_0 represents the hypothetical time required for the dimensions of the cluster, released instantaneously as a point source, to grow to those of the deployment pattern (Csanady 1973). In 2-D Fickian diffusion, K_H would be constant. However, previous studies of oceanic diffusion (Okubo 1971) demonstrate that this coefficient increases with the scale, l, of the cluster as

(8a) $K_H(m^2 \cdot s^{-1}) = 0.579\, l^{1.15}$

where l is arbitrarily defined by

(8b) $l(km) = 3\sigma_{rc}$

(For a Gaussian distribution of particles, 95% of the total number of particles is contained within a diameter of $3\sigma_{rc}$.)

The temporal variations of σ_{rc}^2 and l during the August 1983 experiment (Fig. 14a) reveal an erratic upward trend of the mean square displacement from the centroid as the scale increases from 20 to 50 km. Results for April 1983 and May 1984 show similar behaviour over a slightly larger range of scales. By contrast, these quantities increase more smoothly over the smaller, shorter experiment in May 1985 (Fig. 14b). In order to estimate K_H, the virtual time origin for a point source release was first estimated from the mean square displacement of the initial deployment pattern (σ_0^2) according to Okubo's (1971) formula (in present units).

$$(9)\quad \sigma_0^2(km^2) = 1.08 \times 10^{-12} t_0^{2.34}.$$

Note that this approach assumes that the adjustment of the cluster to a balanced, asymptotic ($t \to \infty$) distribution is immediate upon deployment so that subsequent behaviour reflects the large-scale dispersion rates in the field (Csanady 1973). Two estimates of the apparent diffusivity were then calculated from (1) the final value of mean square displacement, $\sigma_{rc}^2 = \sigma_E^2$, in

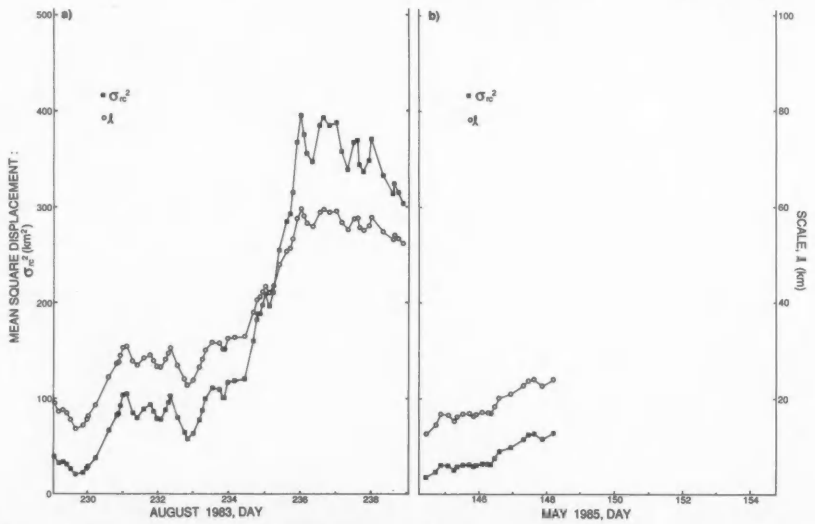

FIG. 14. Time series of mean square displacement (σ_{rc}^2) of selected drogue clusters about centroid and scale of clusters ($l = 3\sigma_{rc}$): (a) day 229–239; August 1983; five drogues, (b) day 144–148; May 1985; six drogues.

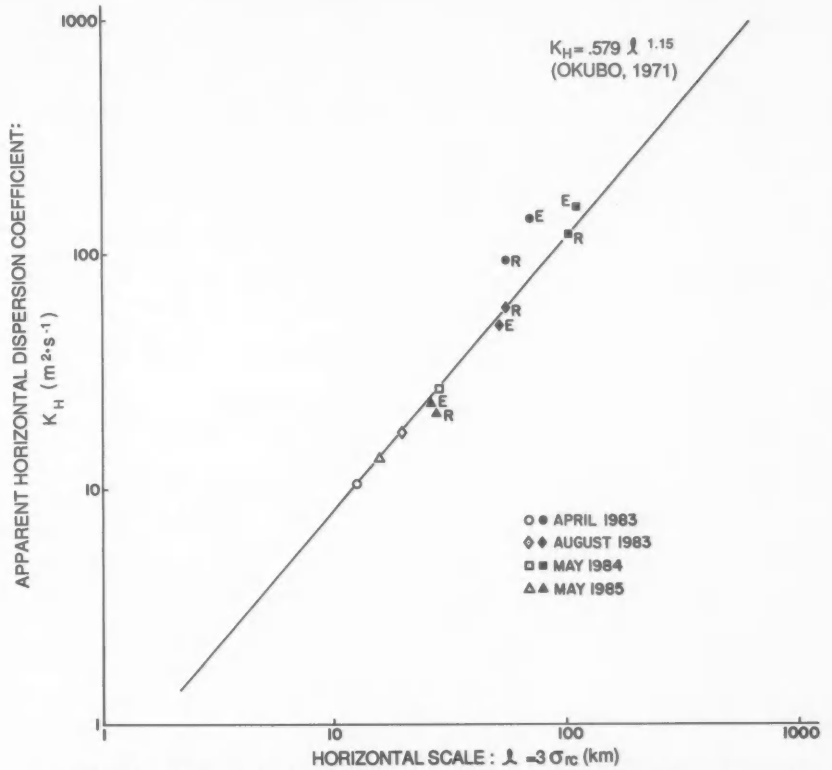

FIG. 15. Variation of apparent horizontal dispersion coefficient, K_H, with scale of drogue cluster. Open symbols represent initial deployment scales, solid symbols represent final state of cluster. In final state, E represents K_H calculated from last measured value of σ_{rc}^2, R represents calculation based on linear regression of σ_{rc}^2 versus time. Solid line represents Okubo's (1971) formula.

the experiment and (2) an approximation to the final value, $\sigma_{rc}^2 = \sigma_R^2$, derived from a linear least squares fit to the square displacement data versus time.

The second technique gives a more reasonable estimate of the trend in the σ_{rc}^2 time series in the face of large oscillations as in Fig. 14a. Comparison of the range of apparent diffusivities with the anisotropic values derived from the DKP analysis (Table 4) indicates that the magnitudes are comparable provided the value, $c = 0.1$, is used to compute K_x and K_y. Furthermore, the variation of K_H with the scale of the cluster is consistent with Okubo's (1971) formula (Fig. 15). Thus the horizontal diffusivity on the scale of Browns Bank appears to be reasonably isotropic and lie in the range of 50–100 $m^2 \cdot s^{-1}$.

Discussion

The validation of Okubo's (1971) formulae (7–9) has important implications for surface-layer dispersion on Browns Bank. Given the initial dimension, $l_0 = 3\sigma_0$, of a patch of buoyant particles such as fish eggs, the horizontal spread of that distribution is governed by,

$$\sigma_{rc}^2(\text{km}^2) = 1.08 \times 10^{-12}(t + t_0)^{2.34},$$

where t_0 is defined by equation 9, and the associated time-varying diffusivity is calculated from equation 7. EG & G (1979) have estimated much larger diffusivities ($500 \leq K_H \leq 10\,000$ $m^2 \cdot s^{-1}$) from drogue clusters of similar scale on Georges Bank, but they did not account for the virtual origin associated with the initial distribution. Nevertheless, their estimates of K_H seem much too large. On the other hand, after accounting for differences in the factor c (they used $c = 1.0$), the EG & G estimates of K_x, K_y are smaller than those in Table 4.

The physical mechanism governing surface layer dispersion is presently unknown. Zimmerman (1986) has pointed out that in energetic tidal regimes, horizontal dispersion coefficients in the range 100–1000 $m^2 \cdot s^{-1}$ may be produced by either (1) a cascade of vertical and horizontal shear dispersion processes, or (2) "Lagrangian chaos" which requires no genuine turbulence. Further, he identifies two types of chaos associated with (1) spatial randomness in the Eulerian velocity field or (2) nonlinear coupling of fluctuating and residual components of that field through the Euler-Lagrange Transformation ("deterministic chaos"). In the former case, horizontal diffusivities associated with tidal random walk are characterized by the residual velocity scale (u_0); the integral correlation length scale, L, of the residual field; and the tidal excursion, U/ω. For small values of $\lambda \equiv U/\omega L \ll 1$, the dispersion coefficient is given approximately by

$$K_H \approx \lambda^2 u_0 L.$$

If the integral length scale is taken as the Browns Bank gyre diameter, $L = 40$ km, then, with $u_0 = 0.1$ $m \cdot s^{-1}$ and $U/\omega = 5$

km, the estimated diffusivity, $K_H \approx 63$ m^2·s^{-1}, is fully consistent with the observed values in Table 4 and Fig. 15.

In the context of a simple Fickian model for symmetric diffusion over a circular bank (Appendix), the time scale for diffusive loss of particles in the surface layer would be $b^2/K_H \equiv L^2/4K_H = 46$ d, where b is the bank radius and $K_H = 100$ m^2·s^{-1} is a representative diffusivity. More quantitatively, the model reveals that during a typical recirculation time of 10 d on the western cap, roughly 50% of the total number of particles (initially uniform) is lost from the bank. The August 1983 dispersion study suggests that this rate of loss may be enhanced in the vicinity of the northern flank, perhaps because of the horizontal shear between the clockwise gyre and the inshore flow into the Gulf of Maine. Furthermore, by comparing results with different initial conditions, model calculations illustrate the importance of knowing the distribution of sources on the bank in order to interpret the evolution of the concentration fields. In the case of live particles (e.g. eggs and larvae), a simple density-dependent form of natural mortality may also be included by multiplying the zero-mortality results by a decaying exponential: e^{-mt}, where m is the mortality rate. A new parameter, $M = mb^2/K$, arising in the dimensionless conservation equation represents the ratio of diffusion to mortality time scales.

As for the Eulerian velocity field, the magnitudes and directions of the surface currents on the 110-m isobath (Fig. 3; Table 2) are compatible with the Lagrangian recirculation times (Table 4) associated with the clockwise gyre over the western cap. In particular, the ratio of cap circumference (≈125 km on 80–100-m isobaths) to the average along-isobath surface current (≈0.16 m·s^{-1}) at C3, C7, and C8 implies a circuit time of 9 d. However, the directions of the Eulerian surface currents on the northern flank do not indicate any mean bias toward off-bank flow to explain the distinct Lagrangian tendency to exit the Bank in this area. Thus, the flux of surface layer particles from the Bank is related to diffusion associated with transient currents rather than a mean Eulerian flow.

The low-frequency current fluctuations at periods of 14 and 28 d from all depths on the C3 moorings are coherent with semidiurnal tidal modulations. However, the off bank currents measured near the bottom on the 110-m isobath (Fig. 3) are exceptionally strong relative to model results (Tee et al. 1988) but consistent with the observations of Magnell et al. (1980) on the northern flank of Georges Bank. The suggestion of Ou and Maas (1986) that such transverse flows may be driven by buoyancy fluxes associated with the barotropic and baroclinic tidal interactions with the sloping sides of a bank is supported by (1) the coherent modulations at 14 and 28 d, and (2) the stronger cross-isobath currents observed on the northern flank (especially C7) where the bottom slopes and baroclinicity are greater. It is interesting to note, however, that according to this 2-D model, the Eulerian mean is not associated with cross-isobath property transport since the mean Eulerian flux is exactly cancelled by the tidal eddy flux.

Conclusion

The primary conclusions of this study are summarized as follows:

(1) The mean Eulerian currents at the surface and mid-depth on the 110-m isobath confirm the existence of a clockwise gyre around the western cap of Browns Bank. On a seasonal basis, the current magnitudes of order 0.1–0.2 m·s^{-1} are relatively uniform over the upper water column, but during the arrival of pulses of low salinity water from the Scotian Shelf, substantial geostrophic shear may develop on the northern flank. Strong cross-isobath flow measured near the bottom is consistent with that observed on the northern flank of Georges Bank and may be related to interactions of barotropic and/or baroclinic tides with the steep sides of the Bank.

(2) The low-frequency current variability on Browns Bank is related to wind and tidal forcing. In the monthly (28 d) and fortnightly (14 d) spectral bands, the wind and tide each contribute 30–40% of the total variance whereas in the synoptic bands (2–10 d) the wind forcing alone contributes 60–80%. The absence of tidal modulations in the synoptic bands suggests that the coupling between wind and tide observed on Georges Bank by Magnell et al. (1980) is not found on Browns Bank.

(3) Some Lagrangian drift tracks support the gyre circulation, but a high degree of temporal and spatial variability is also evident. Estimates of the steady wind-driven response can qualitatively account for some features of the observed tracks (e.g. by promoting or opposing exit from the Bank region). During the summer period 1983, the estimated time (10 d) required for a buoy to circulate around the western cap between the 80- and 120-m isobaths was comparable with the observed residence time (14 d), which means that few complete circuits were executed. The preferred exit region for the drifters is located on the northern flank, particularly the northwest corner of the Bank, but there is no evidence for a mean off-bank Eulerian flow at the surface in this area.

(4) Differential kinemetic properties (DKP) computed from the drogue cluster experiments satisfy simple vorticity balance and thereby give credibility to the analysis. Horizontal diffusivities (K_x,K_y) computed from the DKP residuals are roughly isotropic and consistent with measures of the apparent diffusivity, K_H, calculated from the mean square displacement of the drogues about the centroid (Okubo 1971). With proper accounting for the virtual origin (t_0) of the cluster dispersion, variations of K_H with the cluster scale (l) closely fit Okubo's formula, which suggests $50 \leqslant K_H < 100$ m^2·s^{-1} for patches on the scale of the western cap.

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Appendix

Surface Layer Dispersion of Buoyant Particles on a Circular Bank

To gain some insight into the dispersion time scales over Browns Bank, consider a Fickian diffusion model for the evolution of an annulus of buoyant particles uniformly distributed over a mixed layer of constant depth and centered over a circular bank of diameter $2b$. The concentration of particles, $C(r,t)$, is governed by the equation

$$\text{(A1)}\quad \frac{\partial C}{\partial t} = \frac{K}{r}\frac{\partial}{\partial r}\left(r\frac{\partial C}{\partial r}\right)$$

where r is the radial dimension, t is the time, and K is the (constant) horizontal diffusivity. The boundary conditions for C are

(A2) $C(0,t)$ bounded

(A3) $C(r,t)$bounded as $r\to\infty$.

The initial condition for particles uniformly distributed between $r=a$ and $r=b$ is

(A4) $C(r,0)=G[H(r-a)-H(r-b)]$,

where H is the Heaviside function and G is the initial concentration. Conservation of the total number of particles, Q, implies,

$$\text{(A5)}\quad Q = 2\pi\int_0^\infty rC\,dr = 2\pi\, b^2\, G = \text{constant}$$

The solution to (A1)–(A4), obtained by Laplace transform techniques is

$$\text{(A6)}\quad C(r,t) = \frac{2G}{\pi}\int_0^\infty \frac{J_1(u)}{uD}\left[e^{-\frac{u^2tK}{b^2}}J_0\left(\frac{ur}{b}\right) - e^{-\frac{u^2tK}{a^2}}J_0\left(\frac{ur}{a}\right)\right]du,$$

where $D(u)=J_1(u)Y_0(u)-J_0(u)Y_1(u)$ and J_0,J_1 and Y_0,Y_1 are Bessel functions of the first and second kind, respectively. From this solution it is possible to compute the total number of particles (per unit depth) on the bank versus time

$$\text{(A7)}\quad B(t) = 2\pi\int_0^b rC\,dr$$

$$= 4\,b^2G\int_0^\infty \frac{J_1(u)}{uD}\left[e^{-\frac{u^2tK}{b^2}}J_1(u) - \frac{ae}{b}^{-\frac{u^2tK}{a^2}}J_1 \times\left(\frac{ub}{a}\right)\right]du,\ (0<a<b)$$

$$= 4\,b^2G\int_0^\infty \frac{J_1^2(u)}{u^2D}\,e^{-\frac{u^2tK}{b^2}}\,du,\ (a=0)$$

If live particles (e.g. fish eggs and larvae) are to be considered, it is possible to include a simple density-dependent mortality term of the form, $-mC$, to the right hand side of equation A1. It is easy to show that the solution for this case may be obtained by simply multiplying the right hand sides of A5 to A7 by e^{-mt}. The character of this solution is governed by an additional dimensionless parameter: $M=mb^2/K$, which represents the ratio of diffusion to mortality time scales.

For the western cap of Browns Bank, where $b\sim 20$ km and $K=K_H\sim 100\ \text{m}^2\cdot\text{s}^{-1}$ is a representative value of the diffusivity, the timescale for diffusive loss from the Bank is,

$$T_H = \frac{b^2}{K_H} = 46\ \text{d}.$$

Figure 16 shows the evolution of the radial concentration profile with dimensionless time (i.e. scaled by T_H) for three different initial distributions. When the particles initially cover the entire bank (Fig. 16a), the radial gradient (off-bank particles flux) is everywhere negative (positive) and the central concentration

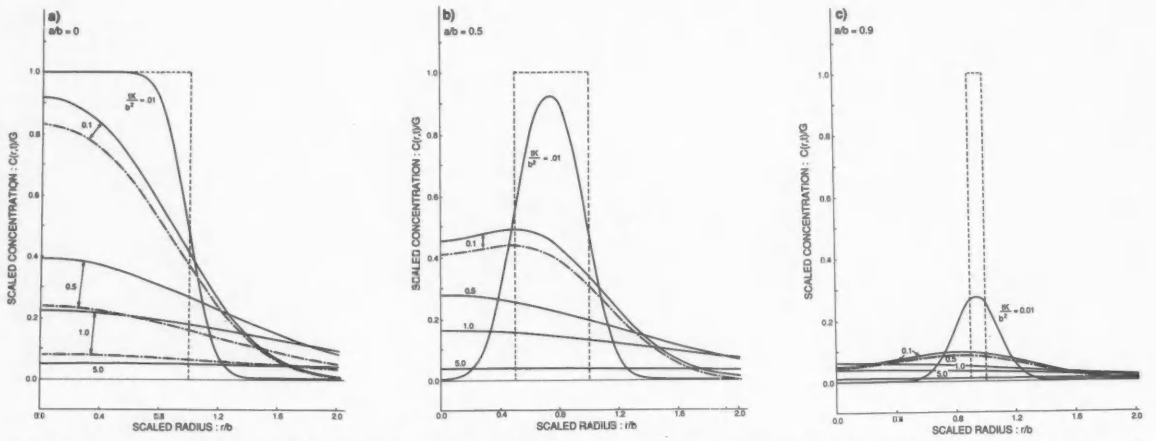

FIG. 16. Temporal evolution of scaled radial concentration profile for various initial distributions: (a) a/b = 0.0, (b) a/b = 0.5, (c) a/b = 0.9. Dashed line indicates initial distribution. Elapsed time is normalized by the diffusive time scale, $T_H = b^2/K$. Dash-dotted curves represent selected profiles corrected for natural mortality in the case $M = mb^2/K = 1$ (see Appendix).

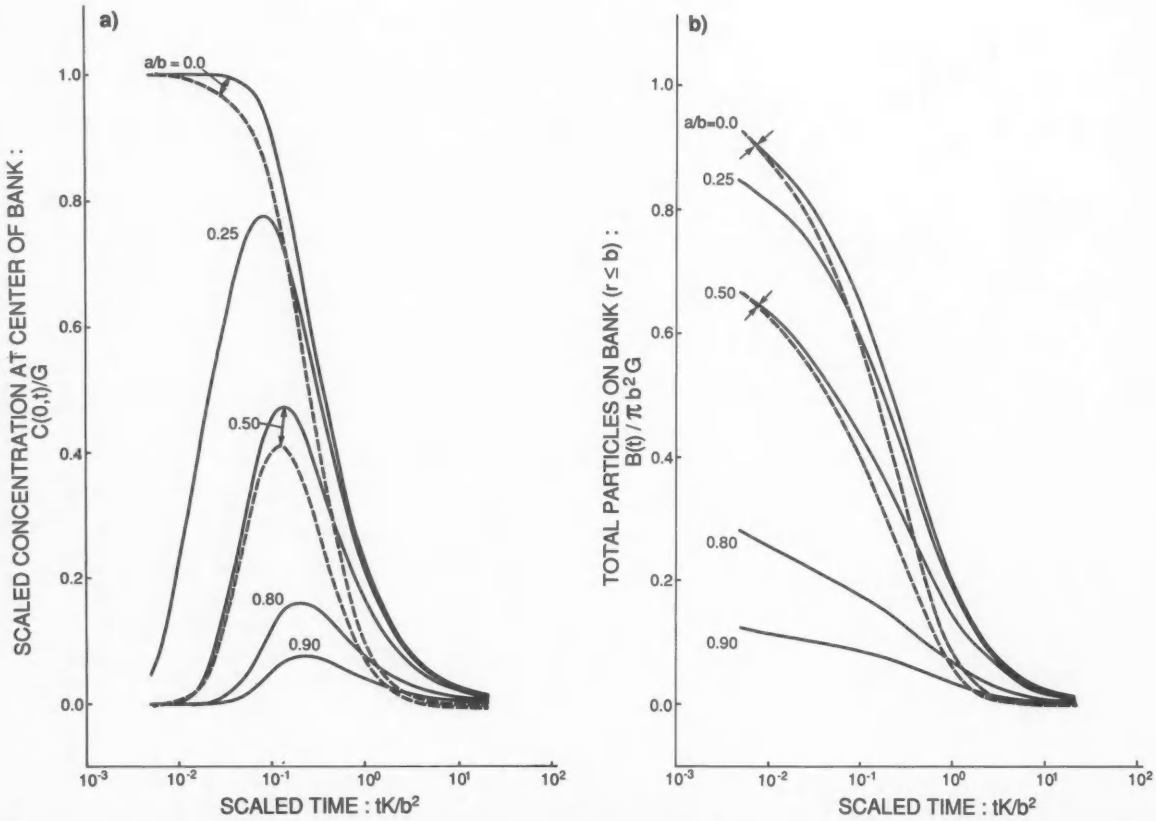

FIG. 17. (a) Temporal variation of central concentration on the bank for various initial distributions. (b) Temporal variation of total number of particles on the bank, $r \leq b$. Dashed curves represent selected time histories which have been corrected for natural mortality in the case $M = mb^2/K = 1$ (see Appendix).

decreases monotonically with time. However, when the intitial concentration lies in an annulus (Figs. 16b,c) the initial particle flux for $r<(a+b)/2$ is directed toward the center of the bank where the concentration builds up until it is sufficient to reverse the gradient at $t\sim 0.5\,T_H$. Thus although the timescale for change is constant, the character of local variations in concentration depends strongly upon the initial distribution. For example, if the buoyant particles were fish eggs newly spawned at $t=0$, it would be important to know whether they were released over the entire bank or just over the flanks in order to interpret their observed distribution with time. Also included in Fig. 16 are selected concentration profiles which have been corrected for mortality in the case $M=mb^2/K=1$, that is when the mortality and diffusive time scales are equal. Clearly if the loss rates are comparable, both effects have to be accounted for in interpreting observed distributions.

For various initial conditions, Fig. 17 depicts the temporal variations of (1) the central concentration on the bank, and (2) the total number of particles within $r\leq b$. Notice that when $a\neq 0$, *the central concentration peaks at some time of the order* $t_p\sim 0.1\,T_H$ which increases with a/b. The total number of particles, $B(t)$, is normalized by that initially found in a uniform distribution over the bank ($\pi\,b^2G$) so that to estimate the relative loss of particles, the values in Fig. 17b should be rescaled by $b^2/(b^2-a^2)$. However, it is clear from the curve for an initial uniform distribution ($a/b=0$) that 50% of the total is lost from the bank at $t\sim 0.2\,T_H$ and that only 20% remains within $r=b$ at $t=T_H$. Thus significant changes in the surface layer distribution of buoyant particles occur over periods of time an order of magnitude smaller than T_H. Again the incorporation of mortality for the case $M=1$ has a marked effect on both the central concentration and total particles on the bank at times comparable to the diffusive time scale.

Copepod Production on the Scotian Shelf based on Life-History Analyses and Laboratory Rearings[1]

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McLaren, I. A., M. J. Tremblay, C. J. Corkett, and J. C. Roff. 1989. Copepod production on the Scotian Shelf based on life history analyses and laboratory rearings. Can. J. Fish. Aquat. Sci. 46: 560–583.

We estimated monthly and annual production of 10 copepod species (>99% of copepod biomass) from Emerald Bank, Scotian Shelf, by use of numerical and weight changes between samples for *Calanus* spp., and by applying daily growth rates based on stage durations and weight increments between stages for others. Of these others, stage durations were estimated from generation intervals inferred from samples of *Metridia lucens*, *Pseudocalanus newmani*, and *Oithona similis*. For species without evident cohorts, notably *Centropages typicus* and *Paracalanus parvus*, we used published temperature-dependent durations. Production in dry weight was estimated as ca. 0.44 $g \cdot m^{-3} \cdot yr^{-1}$ (39 $g \cdot m^{-2} \cdot yr^{-1}$), with peaks in May (largely *Calanus* spp.) and September (largely *C. typicus*, *P. parvus*, and other warm-water forms). All species except *C. finmarchicus* and *O. similis* had annual rates 2–4 times those predicted by the Banse-Mosher allometric relationship between production/biomass ratios and adult body mass. This deviation is not attributable to assumptions in our analyses. Annual copepod production is broadly similar to recent estimates by others using similar methods for Georges Bank, Passamaquoddy Bay, N.B., and the North Sea.

Les auteurs ont estimé les productions mensuelles et annuelles de dix espèces de copépodes (comptant pour plus de 99 % de la biomasse de copépodes) du banc Emerald, sur le plateau Scotian, en utilisant des variations numériques et de poids entre des échantillons pour *Calanus* spp. et en appliquant les vitesses de croissance journalière d'après les durées de stade et les augmentations de poids entre les stades pour les autres espèces. Parmi ces autres espèces, les durées des stades ont été estimées pour des intervalles de génération déduits à partir d'échantillons de *Metridia lucens*, *Pseudocalanus newmani* et *Oithona similis*. Pour des espèces ne présentant pas de cohortes évidentes, notamment *Centropages typicus* et *Paracalanus parvus*, les auteurs se sont servis de données publiées sur les durées dépendantes des températures. La production a été estimée en poids sec à environ 0,44 $g \cdot m^{-3} \cdot an^{-1}$ (39 $g \cdot m^{-2} \cdot an^{-1}$) avec des maximum en mai (essentiellement *Calanus* spp.) et en septembre (essentiellement *C. typicus*, *P. parvus* et autres formes d'eaux tempérées). Toutes les espèces, sauf *C. finmarchicus* et *O. similis*, ont présenté des vitesses annuelles de 2–4 fois supérieures à celles qui avaient été prévues par la relation allométrique de Banse-Mosher entre les rapports production/biomasse et masse corporelle adulte. Cette déviation n'est pas attribuable à des hypothèses formulées au cours des analyses. La production annuelle de copépodes est en gros semblable aux récentes productions estimées par d'autres chercheurs à l'aide de méthodes semblables pour le banc Georges, la baie Passamaquoddy au N.-B. et la Mer du Nord.

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Secondary production has long been understood as growth of biomass, whether or not that biomass is retained by the producers. However, zooplankton production in the sea has only rarely been adequately estimated. Partly this is because direct measurements of growth are difficult or tedious in natural populations of very small animals, and extension to nature of growth rates measured in the laboratory is thought to be risky. Instead, perhaps stemming from Lindemann's (1942) original definition of production as consumption by successive trophic levels, there has been great emphasis on feeding rates by zooplankton in the sea. Parallel studies of the physiology (notably respiration) of zooplankton have often had the explicit aim of estimating growth and production rates by difference (Huntley and Boyd 1984).

Another current enthusiasm in biological oceanography reflects allometric relationships of biological dynamics to body

[1]Fisheries Ecology Program Contribution Number: 2.

size (see Peters 1983). It would indeed be convenient if processes of production in the sea could be quantified by abandoning a plethora of biological circumstantiality in favor of system descriptors such as biomass–size spectra, preferably garnered instrumentally.

Davis (1987) has forcefully argued that estimation of species-specific growth rates of zooplankton may be the only route to accuracy in measurement or prediction of zooplankton production. As he points out, the use of more general or abstract models of production can no longer be defended on practical (or, arguably, philosophical) grounds with the advent of adequate computing power. Essentially the same view is taken by Middlebrook and Roff (1986).

This study uses laboratory and life-history data to estimate production by the 10 most important species of copepods in the waters over Emerald Bank, on the Scotian Shelf, in 1979–80. We believe that the estimates are as accurate as those available for any offshore marine area. There are shortcomings in our analyses and results, but they are given in sufficient detail that others could make estimates using improved data or different methods.

Materials and Methods

Study Areas, Sampling Methods and Sample Treatments

The collecting stations, dates, and sampling methods for the 31 samples from Emerald Bank have been described in Tremblay and Roff (1983b). Briefly, unmetered vertical hauls were made from known depths with 250-μm mesh nets at three or four stations on and around the Bank during eight cruises in 1979–80. These were used as a basis for estimating absolute numbers·m^{-3}. Filtration efficiencies of these nets were tested as slightly less than 100%, but the coarse mesh undersampled small species and stages. Parallel 64-μm mesh nets were used to correct for numbers of small species. More extensive sampling (Tremblay and Roff 1983b; Fig. 1; Table 2) indicated that copepod biomass averaged somewhat larger in the samples used for production estimates (ca. 32.5 mg·m^{-3}) than on the rest of the Scotian Shelf (ca. 24.3 mg·m^{-3}), but that size compositions were widely similar.

In order to examine the generality of life-history patterns underlying production of copepods elsewhere on the Scotian Shelf, similar series of vertical hauls were made during 1979 in 1983–85 over or around Browns Bank, ca. 130 nm southwest of Emerald Bank (Fig. 1). In 1979, Hensen nets of 64-μm mesh (mouth diameter 30 cm, max. diameter 40 cm, filtering cone 1.3 m long) were hauled slowly (0.2–0.5 m·s^{-1}) from 10 m, 25m, and near bottom. Because they did not noticeably clog, the samples were used to estimate relative numbers of individuals of all stages of certain smaller species (less satisfactory for larger ones) occupying the three strata: 10–0 m, 25–10 m, the bottom–25 m. These numbers are in turn used to estimate mean depths occupied by some species (Table 1). Also, the stage distributions in the deepest hauls are used to supplement our life-history analyses.

The samples from Browns Bank in 1983–85 were made during extensive studies on the southwest Scotian Shelf by personnel of the Department of Fisheries and Oceans Canada (Fisheries Ecology Program). Samples were obtained by vertical hauls from near bottom (usually 70–80 m) by Hensen-type nets, one of 202-μm mesh (mouth diameter 42 cm max diameter, 70 cm max. diameter, cone length 3 m) and the other of 64-

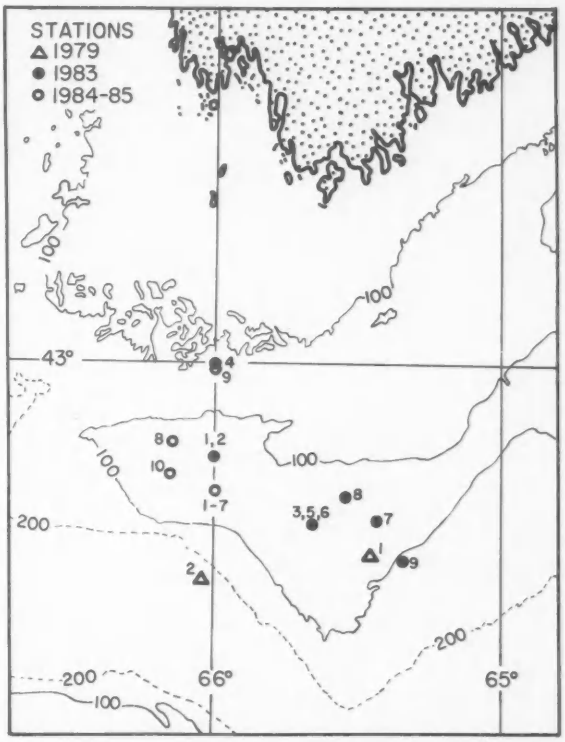

FIG. 1. Stations on and around Browns Bank, southwestern Nova Scotia, from which copepods were collected. Dates of 1979 stations on Table 1. Sequence of 1983 stations are in order of dates given on figure 4 in McLaren et al. (1989a). Sequence for 1984–85 as given in this paper, Fig. 12.

μm mesh (details as above). The samples were not intended to be quantitative, but the larger net is assumed to have retained equally all copepodites and adults of *Calanus* spp., while the smaller net was assumed to have retained equally all stages of *Pseudocalanus* spp. and *Oithona similis*, along with nauplii and youngest copepodites (CI and CII) of *C. finmarchicus*. (Data from Browns Bank on these three species have been largely presented elsewhere (McLaren and Corkett 1986; McLaren et al. 1989a).

Samples were preserved in 5% formalin–seawater. All copepodite stages of some species were identified and enumerated separately in known subsamples, while younger stages of some small species were not counted or were grouped in ways that are evident in the Results. For the Emerald Bank samples, this permitted estimates of absolute numbers·m^{-3} of various stages, while only relative abundances of stages were assessed for life-history analyses of copepods from Browns Bank.

Dry weights of adults and selected stages from the Emerald Bank samples, were obtained and corrected for preservation by assuming 25% loss as described by Tremblay and Roff (1983b). These are variously incomplete (Table 2), because of small numbers and other reasons, and gaps are filled by means described in the Results. Some supplementary weights were obtained in the same way from the Browns Bank samples. We also make extensive use of published weights and lengths in estimating growth rates.

TABLE 1. Numbers of copepods in subsamples (equivalent proportions subsampled from hauls from each depth on given dates) from 64 μm-mesh vertical net hauls in 1979. Numbers of *Pseudocalanus* spp. from the same hauls are listed by McLaren et al. (1988a). Mean depths estimated on assumption that copepods are evenly distributed in each stratum (0–10, 10–25, 25 m–bottom, estimated by subtractions).

Station[a]	Date	Local time	Depth (m)	Numbers (all stages) in subsamples				
				C. finmarchicus	*M. lucens*	*C. typicus*	*O. similis*	*P. parvus*
A1	19 Aug.	0630	10	1	0	193	592	40
			25	18	5	347	1390	126
			90	0	101	447	1753	176
A1	10 Sept.	0815	10	1	0	38	310	18
			25	2	0	89	1104	53
			98	2	14	78	1279	99
A1	11 Oct.	0330	10	0	1	26	37	5
			25	0	0	78	179	21
			85	1	16	116	239	25
A2	6 Nov.	1300	10	0	1	32	83	8
			25	0	3	63	157	23
			225	1	14	154	200	30
Mean depth (dates combined) (m)				—	48	14	14	16

[a]See Fig. 1 for station positions.

Estimating Production

The numbers and dry weights in the samples from Emerald Bank are the raw material for estimating production. One obvious way of doing this has been recognized at least since Boysen-Jensen (1919). Where cohorts can be recognized and followed through time, the amount of production (Pr) over a sampling interval (t–$t+1$) is readily estimated as the mean number ($\bar{N}$, variously estimated) in the cohort during the interval multiplied by the increase in mean weight, $\Delta\bar{W}$, of individuals in the cohort. Rather than use the usual incremental summation method, which implies constantly decreasing growth and survival rates during the interval, we assume constant growth and mortality rates

$$(1)\quad Pr = g(B_{t+1} - B_t)/(g - m),$$

where $g = \ln W_{t+1} - \ln Wt$, $m = \ln N_{t+1} - \ln N_t$, and B_t and $Bt + 1$ are biomasses ($N \cdot \bar{W}$) in the successive samples. In our study, only the samples of *Calanus* spp. were sufficiently representative to permit estimation of production by equation (1). Only adults and copepodites, which are believed to have been equally retained by the nets, were counted. Nauplii contribute a very small fraction of the biomass and do not develop notably more rapidly (Corkett et al. 1986), and therefore contribute little to production. We will examine consequences of alternative assumptions about growth and mortality in our accounts of *Calanus* spp. (see Results).

Samples of other species could not be treated by the above procedures for two reasons: (1) in some, cohorts were difficult or impossible to recognize; (2) in others, cohorts could be recognized, and generation lengths inferred from the samples, but stages were grouped or unequally sampled (most younger copepodites missing) so that numbers and mean weights in cohorts were too distorted for the application of equation (1). These required alternative approaches using estimates of growth rates. Such approaches have generated much confusing and overly technical discussion in the literature that is well clarified by Kimmerer (1987), who writes in the context of copepod production. We use his terminology and symbolism throughout. If biomasses (B) and growth rates using a time scale of days can be estimated (either instantaneous, g, or specific daily finite growth rates, $G = e^g - 1$, are quite acceptable for copepods in which biomass changes little during a day), then production rate is given by

$$(2)\quad PR = \Sigma G_i B_i$$

where i refers to particular life stages with different growth rates in the population. There is no need to measure mortality or natality rates (except as the direct contribution of eggs to production) as has sometimes been supposed.

Biomasses (B_i) of productive stages (e.g. excluding adult males) are readily estimated from our samples. Earlier stages of small species were undersampled, but again these have small biomasses, development rates similar to those of older stages, and add little to production. Estimating G_i remains the major task in estimating production rate. There are two components to this estimation. First, the increase in weight between successive stages must be measured, and second the interval between the stages must be known. Weights from the Emerald Bank samples generally had to be augmented by a variety of published and unpublished material to obtain estimates of growth increments between stages. However, we require only relative weights of successive stages; thus volumes based on prosome lengths can be used where weight estimates are inadequate. Since samples of smaller species were mostly adult and late copepodite stages, we use growth increments between those stages where appropriate.

The second requirement, that of estimating the time interval between stages, is much more difficult. Possibly the most promising approach is to determine short-term molting rates immediately after capture under in situ conditions (e.g. Burkill and Kendall 1982; Runge et al. 1986), but this was not done for the Emerald Bank populations. Cohorts in samples can sometimes be recognized by abundance modes in stage-frequency distributions, but this is often not possible when young stages are badly undersampled. However, among copepods there are often marked seasonal differences in body size, as influenced by temperature and perhaps food supply during development. With some degree of synchrony in life cycles, there will be intervals when sizes of long-lived adult females

TABLE 2. Dry weights (micrograms) of common copepods from Emerald Bank in 1980. Values are corrected for preservation assuming a 25% loss. Numbers in parentheses are: number of replicates/no. of stations where replicates obtained.

Species	Stage	19–20 Feb.	24 May	18 June	1 Aug.	25–26 Aug.	15–16 Sept.
C. finmarchicus	Ad♀	197 (11/3)	254 (12/14)	236 (1/1)	161 (1/1)	—	—
	CV	157 (7/3)	142 (8/4)	122 (8/4)	139 (6/1)	139 (17/2)	133 (8/1)
	CIV	—	35 (8/4)	42 (8/4)	58 (6/1)	54 (3/1)	53 (3/1)
	CIII	—	16.1 (8/4)	13.5 (7/4)	17.1 (3/1)	—	—
	CII	—	5.5 (8/4)	—	7.1 (3/1)	—	—
	CI	—	2.7 (8/4)	—	3.2 (3/1)	—	—
M. lucens	Ad.♀	91 (4/2)	110 (8/4)	125 (8/4)	117 (2/1)	123 (3/1)	74 (6/1)
	Ad.♂	—	—	—	—	—	29 (3/1)
	CIV–V	—	—	—	—	—	17.7 (3/1)
C. typicus	Ad.♀	24 (4/2)	—	40 (3/2)	41 (2/1)	27 (3/1)	19.6 (6/1)
	Ad.♂	16.8 (1/1)	—	—	—	—	18.8 (6/1)
	CV	12.4 (2/1)	—	—	—	10.3 (3/1)	9.7 (3/1)
	CIV	—	—	—	—	5.2 (3/1)	5.5 (3/1)
P. newmani	Ad.♀	11.4 (11/3)	10.3 (8/4)	9.4 (8/4)	9.1 (20/4)	10.1 (6/2)	7.4 (6/1)
	CIV–V	9.7 (9/3)	6.3 (8/4)	6.8 (8/4)	—	—	—
	CI–III	—	2.2 (6/3)	—	—	—	—
P. parvus	Ad.♀	7.7 (1/1)	—	6.0 (7/4)	6.7 (3/1)	5.6 (3/1)	5.4 (6/1)
O. similis	Ad.♀	2.4 (5/3)	1.7 (8/4)	2.3 (7/4)	1.8 (3/1)	1.7 (3/1)	2.7 (3/1)
	CI–V	2.1 (4/3)	1.0 (8/4)	—	—	—	—

are more or less stable, punctuated by sharper changes after substantial changeover of generations. Size–frequency distributions may be roughly normal in some samples, and decidedly non-normal in others. Furthermore, as levels of significance assigned to size differences within and between different generations would have to be based on a priori knowledge to be meaningful, statistical methods cannot be used to define different generations (see also discussion of this in McLaren 1978). Rather, we discriminate cohorts by inspection, which we hope will be equally possible for readers. We do not assume that the entire population is in a designated generation in a given sample; indeed, there is certainly considerable generation overlap occasioned by different individual histories of conditions of food and temperature. We do assume that individuals at a given time and place are experiencing the same conditions for growth as indicated by the prominent cohorts. For those species in which cohorts seemed sufficiently evident, we approximated the times of spawning and recruitment of successive generations. Then, laboratory data on the relative duration of stages within a generation were used to estimate the absolute duration of individual stages within such approximated generation times.

For other species, there was little or no evidence of cohorts. To these we applied growth rates that assume that individuals are developing and growing at temperature-dependent rates. First we estimated depths at which they were living and the temperatures (Fig. 2; nearest 0.5°C) that they may accordingly have been experiencing when captured. Then, where possible, we used temperature-dependent stage durations estimated in the laboratory under conditions of excess food. Because of its empirical convenience, we use Bělehrádek's temperature (T) equation to describe durations (D) at any temperature in the manner described by McLaren (1978),

$$(3)\quad D = a(T - \alpha)^{-2.05}.$$

This permits, for example, the estimation of durations of older stages from fitted values of α for embryonic development and measurements of stage durations at a single temperature (see McLaren 1978; Corkett et al. 1986; McLaren et al. 1989b for applications of this rule of equiproportional development). Having obtained the duration D in days of a given stage at a given temperature, finite growth rate per day, G_i, can be estimated for that stage from the initial and final weights (W) of the stage, or more readily from mean sample weights of two successive stages, i and $i + 1$,

$$(4)\quad G_i = (W_i + 1/W_i)^{1/D} - 1.$$

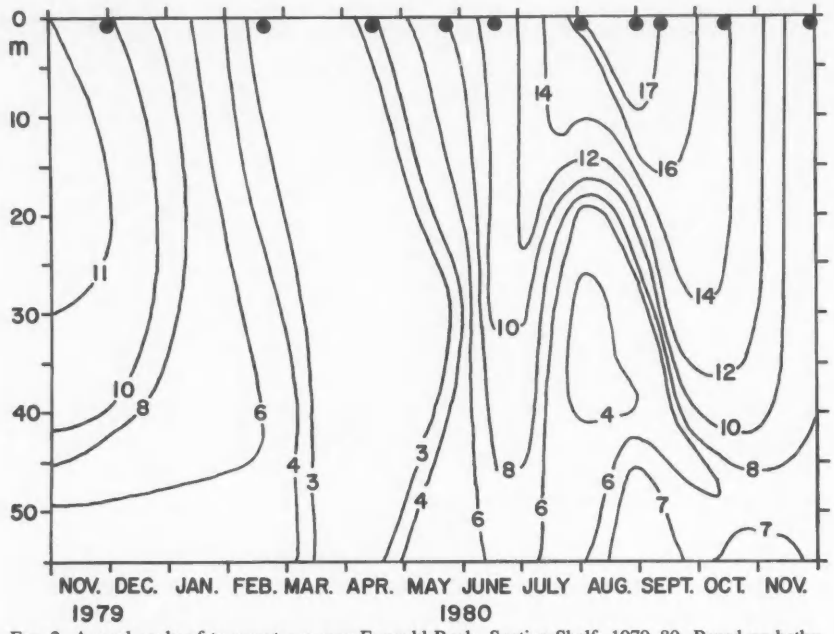

FIG. 2. Annual cycle of temperatures over Emerald Bank, Scotian Shelf, 1979–80. Based on bathythermograph tracings on the dates marked by filled circles, except that April temperatures were estimated from the means of those on 18 April 1979 and 10 April 1981.

This can be used as such in equation (2). Multiplied by 100, it is readily seen as percent increase in biomass per day. For some species we will show that development and growth rates for different stages may be sufficiently similar so that little error is introduced by assuming a common *Gi* for all copepodite biomass in a given sample.

We recognize that our production estimates based on temperatures (three species) are maximal, although we will offer evidence that much production in them may indeed be uninhibited by food shortages. Where we base production estimates on observed cohorts in some other species, we examine evidence for temperature-dependence of their generation lengths.

Adult males are treated as non-productive biomass. In some species they are short-lived and so rare that, even where not separately identified, their presence need not be accounted for. The production of egg matter by females is a contribution to production that cannot be measured as increase in weight in that stage. There are indications in some species (e.g. Corkett and McLaren 1978; Sekiguchi et al. 1980; McLaren and Corkett 1981) that maximum rate of production of egg matter per unit female weight is the same as G_i of younger stages. We assume this for a few species, but where possible we estimate rates of production by adult females from a variety of empirical sources.

In estimating integrated production (*IP*) over the year, we either sum the values of *Pr* for the intervals over which equation (1) was applied or, after linear interpolation between daily *PR*'s from equation (2), integrate numerically over months or over the year. More accurate estimates might come from more elaborate interpolation between dates followed by simultaneous integration of biomasses and growth rates. However, given other approximations in our approaches, this does not seem worthwhile; it would also be less readily repeated from our data by readers. Annual P/B ratios for each species are, as usual, total production during the year divided by average biomass (also estimated by linear interpolation between dates) during the year.

Other methods applying to particular species or situations will be considered in Results under those species.

Results

Because of the different models and assumptions used in estimating production for each species, we present our results as species-by-species accounts, in order of their annual productivity. For each species, we first describe the life cycle as inferred from the samples and other evidence. Then follows an account of growth and reproduction, usually leading to estimates of specific daily rates of stage growth and production of egg matter. Finally, the information on life cycles, growth rates, and reproductive rates is converted to estimates of production on or between sampling dates, and these are integrated by the month and for the year.

Calanus finmarchicus

Life cycles

This species outnumbered all others in spring samples. Because of its large size its copepodites were well sampled by the coarse nets. They were distinguished from *C. glacialis* on the basis of size-groups that overlapped only slightly if at all in given samples. McLaren and Corkett (1986) concluded that *C. finmarchicus* on Browns Bank during 1983 was essentially annual in life cycle. Most of the new generation (G_1) "rested" as older copepodites until the early part of the following year, with only a small fraction of females maturing to produce a second generation in summer (G_2). The same pattern was found on Browns Bank in 1984–85; CV was the most prominent stage

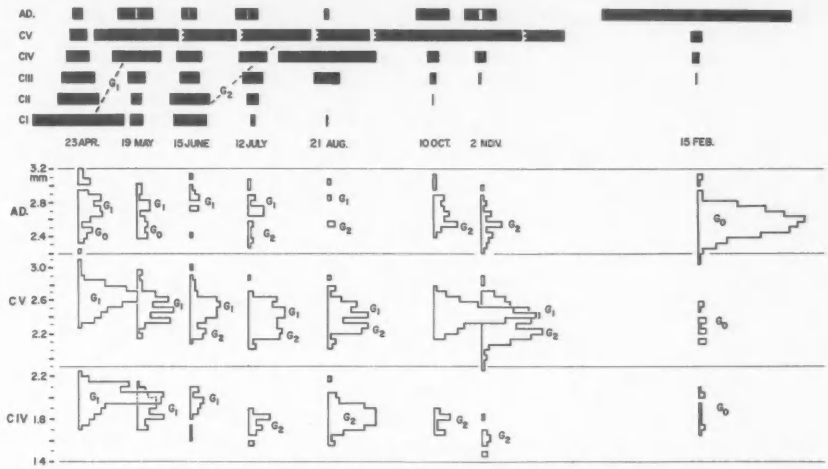

FIG. 3. Annual cycle of *Calanus finmarchicus* on Browns Bank, April 1984 to February 1985. Successive generations labelled G_0, etc. Upper panel: abundances as proportions of stages (males clear section of adult bar). Lower panel: numbers of CIV, CV, and adult females in arbitrary subsamples from samples.

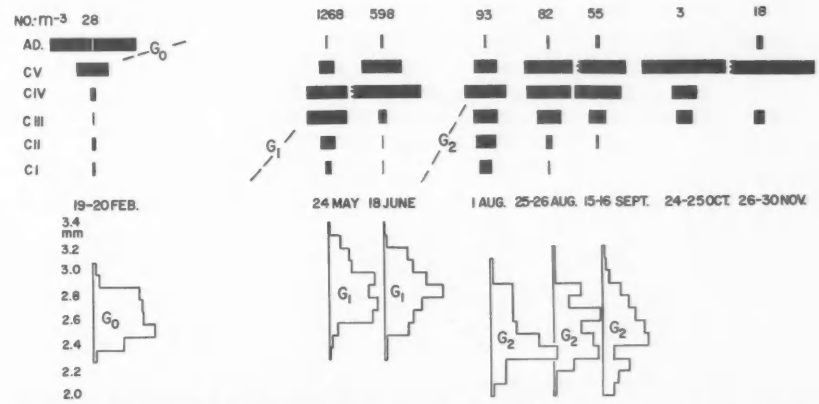

FIG. 4. Annual cycle of *Calanus finmarchicus* on Emerald Bank, 1979–80. Successive generations are G_0, etc. For convenience, Nov. 1979 sample placed at end. Upper panel: proportions of stages. Lower panel is size-frequencies of adult females in proportions.

from mid-May to early November, but augmentation of younger copepodites in mid-June and the subsequent tendency for size bimodalism are evidence for recruitment of a small second generation (Fig. 3).

On Emerald Bank in 1979–80 (Fig. 4) very few animals matured after the late-winter spawning. The very small fraction that did mature in summer could have produced a G_3, but no augmentation of young stages was evident after 1 August. The larger numbers (Fig. 4) in late November 1979 ($18 \cdot m^{-3}$) and February 1980 ($28 \cdot m^{-3}$) compared with late October 1980 (ca. $3 \cdot m^{-3}$) could represent a real difference in the overwintering stock between years. However, many of the "resting" animals apparently leave for deeper waters of the continental slope or basins on the shelf, where they may be an order of magnitude (per unit area) more dense than over the banks (Lewis and Sameoto 1989).

Our inferences about life cycles can be drawn from the frequency distributions of copepodite stages alone, but size distributions require more consideration. We believe that the small size of animals appearing in summer and labelled as G_2 (Fig. 3, 4) reflects their development in warmer waters and perhaps lower food supply of early summer. We are aware of work attributing size bimodalism in late copepodites of *Calanus* species to sexual dimorphism (e.g. Grigg et al. 1987). We did not examine this possibility, but suggest that such an interpretation must account for the fact that the advent of bimodal CV is accompanied by smaller CIV and adults, which seem clearly attributable to a different generation (Fig. 3; see also McLaren and Corkett 1986; Fig. 2).

McLaren (1986) concluded that development of *C. finmarchicus* up to CV on Browns Bank in spring 1983 was predictable from temperatures. For 1984 (Fig. 3), we sketch a trajectory of development from CI on 23 April to CV on 19 May. In waters at ca. 3.5°C during this interval (McLaren et al. 1989a; Fig. 1), development from CI to CV would be minimally 31 d (Corkett et al. 1986), so our approximation is reasonable and

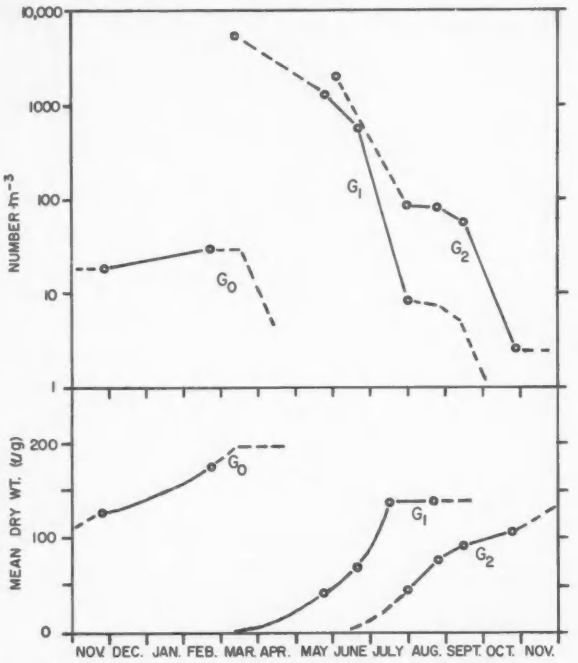

FIG. 5. Numbers and mean weights of animals in successive generations (G_0, etc.) of *Calanus finmarchicus* on Emerald Bank, 1979–80. Unbroken lines connect estimates from samples, dashed lines inferred as described in text.

suggests that G_1 was spawned about mid-March. It is not possible to estimate development rates in summer on Browns Bank (Fig. 3) or at any season on Emerald Bank (Fig. 4), because samples were not critically timed. However, the great majority cleared remained in lipid-rich late copepodite stages through summer and autumn, uninfluenced by prevailing temperatures or food supply.

Growth and Reproduction

Weights of stages of *C. finmarchicus* from Emerald Bank (Table 2) were very similar to those used by McLaren (1986) to estimate growth rates on Browns Bank. However, in using equation (1) to estimate production, there is no need for explicit estimates of growth rates from these weights.

Female *C. finmarchicus* captured on three occasions in May–June on the Scotian Shelf and kept in ambient conditions produced ca. 21, 1.6, and 31 eggs·d^{-1} (Runge 1985). The two higher values were similar to those in excess food in the laboratory. The smaller value was at an area and time of low chlorophyll levels and it is clear that daily rates can be far from maximal. However, we do not use daily rates in estimating production by this species.

Others (e.g. Williams and Lindley 1980), have assumed from Marshall and Orr (1952, 1955) that, although daily rates may respond to short-term food levels, lifetime output might be ca. 250 eggs, or ca. 10 d of maximal production (see above). This is a conservative period for spring diatom blooms in shelf waters (e.g. Horne and Platt 1984; Fig. 5c). Eggs are assumed to weigh 0.6 µg dry weight (Dr. J. A. Runge, Fisheries and Oceans Canada, Maurice Lamontagne Institute, Mont Joli, Que., pers. comm.).

TABLE 3. Production by *Calanus finmarchicus* on Emerald Bank, 1979–80. Growth production by generations (G_0 etc.) based on mean numbers and weight increments of cohorts between successive dates. Egg production based on numbers of females at times of spawning 250 eggs each (see text).

Period	Biomass at start of interval ($mg \cdot m^{-3}$)	Production ($mg \cdot m^{-3}$)			
		G_0	G_1	G_2	eggs
26–30 Nov. to 19–20 Feb.	2.33	1.0			
19–20 Feb. to 24 May	4.72	0.6	72.3		3.4
24 May to 18 June	49.89		25.7		1.2
18 June to 1 Aug.	41.43		4.8	9.4	
1 Aug. to 25–26 Aug.	5.06			2.4	0.3
25–26 Aug. to 15–16 Sept.	6.41			0.5	
15–16 Sept. to 24–25 Oct.	4.88			0.1	
24–25 Oct. to 26–30 Sept.	0.26			0.1	

Production

In order to assess production from changes in numbers and weights, cohorts (generations G_0, etc.) were distinguished in the samples (Fig. 5). The distribution of individuals among generations when they overlap is determined as follows. It is assumed that all G_0 copepodites matured and died before 24 May, when all animals were G_1 (Fig. 4, 5). All animals were taken as G_1 on 18 June (Fig. 4, 5). On 1 August all CI–CIII (Fig. 4) are taken as G_2. By analogy with samples from Browns Bank on 12 July and 21 August (see size-frequencies, Fig. 3), all CIV and one-half CV on Emerald Bank on 1 August are also considered to be G_2. All adult ♀♀ and ♂♂ from 1 August are assumed to be G_2 (see size frequencies on Fig. 4). Thereafter, numbers of "resting" CV in G_1 are assumed to decline in parallel with overall decrease (as shown by dashed-line extension of G_1 on Fig. 5). Numbers of G_0 prior to late November 1979, and of G_2 (which becomes next year's G_0) after October 1980, are assumed to be constant (Fig. 5). Consequences of alternative dispositions among generations are considered below.

The dashed lines initiating G_1 and G_2 on Fig. 5 are estimated numbers prior to their appearance as copepodites. For G_1, it was assumed that all females (adults plus one-half of copepodites = $22.6 \cdot m^{-3}$) present on 19–20 February survived to reproduce 250 eggs each in mid-March. Linear back-extrapolation of the dashed line for G_2 on Fig. 4 suggests its origin in early June. The average of the numbers of females present on 24 May ($8.0 \cdot m^{-3}$) and 18 June ($7.8 \cdot m^{-3}$) was taken as the number present in early June, each producing 250 eggs to initiate G_2. The average of numbers of females of G_2 on 1 August ($1.7 \cdot m^{-3}$) and 25–26 August ($1.5 \cdot m^{-3}$) are assumed to have produced their 250 eggs each during that month, none developing into a detectable G_3. Alternatives to these assumptions are examined below.

Mean weights of cohorts (Fig. 5) are estimated from numbers (Fig. 4) and from weights of stages (Table 2). The mean ratios of weights of successive stages available for all stages on 24 May and 1 August were used to estimate missing weights for some stages on other dates. Weights for 24 October or 26–30 November were assumed to be the same as those for 15–16 September.

Most production (Pr) was estimated separately by generations from numbers and mean weights on successive dates using equation (1). McLaren (1986) showed that growth of *C. finmarchicus* between CI and CV was exponential during the period of temperature-dependent development in spring, and

use of equation (1) implies this is true between all sampling intervals. Constant growth rate is the simplest assumption; it does not imply that growth is uninhibited by food shortages between sampling dates. Similarly, constant mortality rate (per equation (1)) is the simplest assumption, but alternatives will be considered below. The estimates are summed for all time intervals and cohorts to give annual production due to growth. To this is added an amount of egg matter (0.6×250 μg) produced by each female on the assumed dates of reproduction by G_0 in mid-March and G_1 in early June (see above). Females of G_2 are assumed to have produced their 250 eggs in mid-August, but without an ensuing generation. Our estimates (Table 3) show clearly that the bulk of production is due to the growth of G_1 in spring. Total annual production (sum of Table 3) is 122 $mg \cdot m^{-3}$. The mean annual biomass of 14.5 $mg \cdot m^{-3}$ (linear interpolation between dates) yields an annual P/B of ca. 8.

We stress that some of our approximations and assumptions have little effect on our estimates. For example, our assignments of numbers into generations where these overlap shifts a small amount of production as the stages involved are either scarce or non-growing.

For older stages there are two extreme alternatives to the assumptions of exponential growth and mortality between dates: that all growth between sampling intervals occurred before any mortality, or that all mortality occurred before any growth. These most unlikely alternatives yield estimates for 24 May to 18 June (the period of major production by older stages) 47% higher and 30% lower, respectively than the value on Table 3.

The estimates of production by G_1 between 19–20 February and 24 May and by G_2 between 18 June and 1 August are also influenced by assumptions about growth and mortality rates. For these it is impossible that all mortality occurred after growth. The extreme opposite assumption, that all mortality occurred among very young stages before any growth, would reduce production of G_1 by 31% and of the much smaller G_2 by 64% compared with values for these intervals on Table 3.

It also follows from the much larger size of later stages that assuming constant mortality rate reduces the importance of initial size of cohorts (i.e. number of eggs per female). For G_1 in the interval 19–20 February to 24 May, doubling the initial size of the cohort increases production by 33%, and halving the size reduces it by 12%, compared with the value on Table 3. For G_2 between 18 June and 1 August, these changes are 36 and 23%, respectively. The effect of initial cohort size would be reduced even further if we assume declining mortality rates from eggs to copepodites during the interval (see above).

Our estimates of egg production make up only 4% of the annual total. An extreme alternative assumption is that every female produced ca. 25 eggs every day (approximate maximum at 6–8°C, from Runge 1985), although these only gave rise to generations at times indicated; from estimated average daily numbers of females this yields a production of ca. 40 $mg \cdot m^{-3} \cdot yr^{-1}$, much larger than the combined values for eggs on Table 3. We believe this is highly unrealistic (since generations were only recruited during late winter and late spring), but if adopted it would only increase the total annual production by some 29%.

Thus, we believe that our estimates of production by *C. finmarchicus*, dominated as they are by growth of later stages, are reasonably accurate in spite of the lengthy sampling intervals. A more general qualification of any such estimates based on life-history analysis arises if copepodites advected from the bank stay in deeper waters and are not replaced by their equivalents. If earlier copepodites remain on the bank and later ones leave, this would negatively bias our estimates of production based on equation (1). However, the cohort stage distribution does appear quite stable or slowly advancing in late summer and autumn (Fig. 3, 4). Of course even if production is correctly assessed, such departure after the season of high production will inflate the annual P/B ratio.

Metridia lucens

Life history

This large copepod is present throughout the year on Emerald Bank in numbers that vary less than those of other copepods. It also occurred in samples from Browns Bank, but too sparsely for adequate analysis. On Emerald Bank, in spite of probable undersampling of earlier copepodites by the coarse nets, its life cycle seems clear (Fig. 6). An overwintering population, largely small adult females on 19–20 February, spawned a first spring generation (G_1) that contained proportionately more early copepodites on May 24, and more late copepodites and adults by 18 June. Thereafter, G_2 and G_3 seem evident in size distributions of females that are stable over two sampling dates. However, there was little difference between stage-frequency distributions in early and late August, and possibly only a fraction of G_2 matured during this interval. If so, the large increase in numbers and drop in female size in mid-September would reflect recruitment of females from "stalled" G_2 copepodites along with G_3 offspring of those G_2 females that had spawned earlier.

The great increase of young copepodites in late October, and their progression to older copepodites in late November, seem clearly to reflect a new generation (G_4, although possibly with elements of a G_3), which we suggest makes up the overwintering stock that becomes G_0 of the following spring. If four complete generations were involved, we can assume for calculations that G_1 was spawned in early March and that later generations originated at times half-way between sampling dates: G_2 in early June, G_3 in mid-August, and G_4 in early October. An alternative interpretation would be that G_2 was spawned in early June but that most offspring remained "stalled" until early October.

There is additional evidence on life cycles in the sparse but more completely staged samples of *M. lucens* from Browns Bank in 1979 (Fig. 7). In these there was little change between 19 August and 10 September, suggesting that the population was indeed largely "stalled." A progression to maturity occurred in October (= lagging G_2?). More young (= G_3?) also appeared in October and developed further by November.

The first interpretation above implies generation lengths of some 90 d for G_1, 70 d for G_2, and 55 d for G_3, with G_4 ($= G_0$) slowly developing over a 150 d period in winter. The extreme alternative is that G_2 largely "stalled" through August and did not mature in significant numbers until 125 d later in early October. The species evidently lives quite deep (mean ca. 48 m, Table 1), where it would have experienced temperatures of ca. 3–6°C through the year (Fig. 2). We find no published laboratory studies that could be compared with our inferences about generation length. However, minimal generation lengths of other temperate species at 3–6°C (e.g. *Calanus finmarchicus* (Corkett et al. 1986) and *Pseudocalanus moultoni* (McLaren et al. 1989a)) are about 60–90 d, in keeping with our inferences about the generally slow development of *M. lucens*.

Growth and Reproduction

Weights of adult female *M. lucens* on Emerald Bank were obtained for all sampling months except October and Novem-

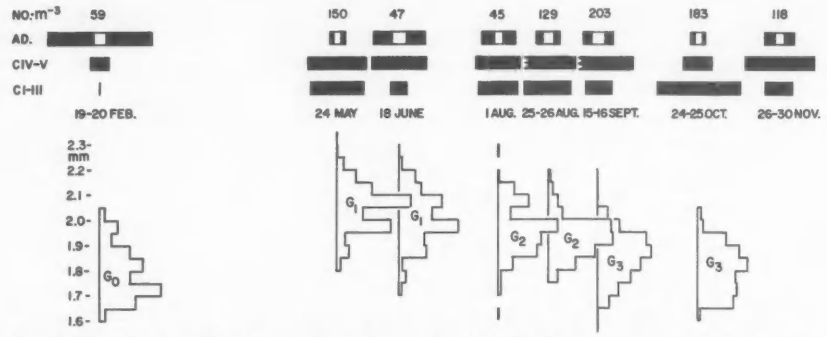

FIG. 6. Annual cycle of *Metridia lucens* on Emerald Bank, 1979–80. Successive generations are G_0, etc. For convenience, Nov. 1979 sample placed after 1980. Upper panel: abundance as proportions of stages. Lower panel: size-frequencies of adult females as proportions.

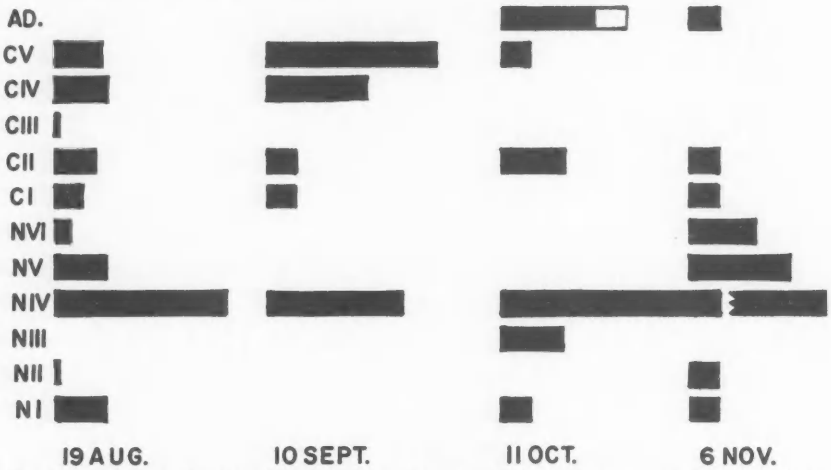

FIG. 7. Proportions of stages of *Metridia lucens* in vertical hauls from near bottom (see Table 1) on and near Browns Bank, 1979. Adult males are clear proportion of bar.

TABLE 4. Estimated daily production rates by *Metridia lucens* on Emerald Bank, 1979–80. Production is daily growth rate multiplied by biomass of all stages except adult males. Alternate assumptions of three or four generations per year described in text.

	Biomass ($\mu g \cdot m^{-3}$)		Daily production rates ($\mu g \cdot m^{-3}$)	
Sample date	cop. + ad.♀♀	ad.♂♂	four generations per year	three generations per year
26–30 Nov.	2656	327	186	186
19–20 Feb.	4070	238	285	285
24 May	3639	301	400	400
18 June	2549	211	376	200
1 Aug.	1966	90	287	153
25–26 Aug.	4119	444	824	330
15–16 Sept.	4430	557	886	354
24–25 Oct.	2490	254	173	173

ber, but males and grouped younger stages were weighed only from the mid-September sample (Table 2). Because of the grouping of stages, these weight data cannot be used to estimate growth increments between stages. A sample from the Scotian Shelf off Halifax, N.S. (Dr. G. Harding, Bedford Institute of Oceanography, Dartmouth, N.S., pers. comm.) yielded the following prosome length ratios: CIV/CIII = 1.28; CV♀/CIV = 1.46; CV♂/CIV = 1.26; ad.♀/CV♀ = 1.38; ad.♂/CV♂ = 1.05. These agree quite well with ratios from Iceland waters (Kanaeva 1962): CII/CI = 1.31; CIII/CII = 1.31; CIV/CIII = 1.34; CV♀/CIV = 1.45; ad.♀/CV♀ = 1.38. Therefore, we use the wet weights of CI (4 μg) and adult females (570 μg) listed by Kanaeva (1962) to approximate daily specific growth rate of copepodites. To do so we assume that copepodite growth

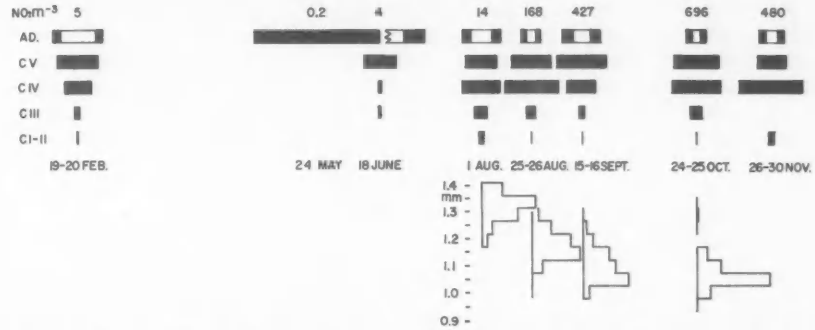

FIG. 8. Annual cycle of *Centropages typicus* on Emerald Bank, 1979–80. Successive generations are G_0, etc. For convenience, Nov. 1979 sample placed at end. Upper panel: abundances as proportions of stages (males clear section of adult bar). Lower panel: size-frequencies of adult females as proportions.

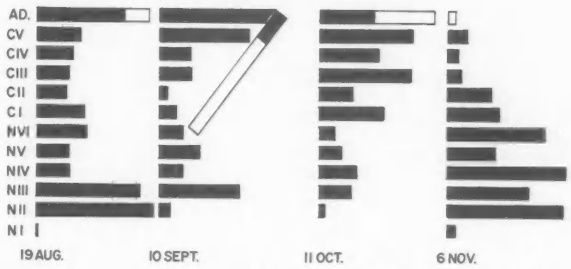

FIG. 9. Proportions of stages of *Centropages typicus* in vertical hauls from near bottom (see Table 1) on and near Browns Bank, 1979. Adult males are clear portion of bar.

rate is constant for a given generation, that CI to maturity is half the generation time, and that each copepodite takes 20% of that period. Assuming four generations, this yields daily growth rates from equation (4) of ca. 11% for G_1, 15% for G_2, 20% for G_3, and 7% for G_4 ($= G_0$). Under the alternative assumption that G_2 completely "stalled" during late summer, we have 11% for G_1, 8% for G_2, and 7% for G_3 ($= G_0$). Both alternatives are presented on Table 4.

No information is available on egg production rates of *M. lucens*. However, we have observed copious egg production by females soon after being brought into the laboratory. We assume that females when present are reproducing maximally, and that weight-specific rate of production of egg matter is equal to the weight-specific growth rate of copepodites.

Production

To estimate biomasses of *M. lucens*, female weights available for most sampling dates are multiplied by proportionate weights of grouped CIV–CV and CI–III copepodites, relative to those of ad. ♀♀ weights in the September sample (Table 2). Missing weights for all stages in the October and November samples are assumed to be the same as those for September. These weights are multiplied by the numbers of adults and grouped CIV–V and CI–CIII (Fig. 6) to obtain biomasses (Table 4).

Specific daily growth rates (G_i) assuming both three or four generations per year (see above under Growth) are applied to combined biomasses (B_i) of copepodites and females (producing egg matter at the same rate) to obtain daily production rates (*PR*) from equation (2). Total annual production (*IP*), estimated by integration after linear interpolation between daily rates (Table 4), is 97 $mg \cdot m^{-3} \cdot yr^{-1}$ for three generations and 133 $mg \cdot m^{-2} \cdot yr^{-1}$ for four generations per year. If part of the population was "stalled" during August–September, while others continued to develop, the intermediate value of 115 $mg \cdot m^{-3} \cdot yr^{-1}$ is our best estimate. Mean annual biomass by similar interpolation is 3584 $\mu g \cdot m^{-3}$, for an annual P/B ratio (intermediate value of *IP*) of 32.

TABLE 5. Intervals between successive stages in *Centropages typicus*, based on Smith and Lane (1985, 1987). These intervals (*D*) are used to estimate values of *a* of Bělehrádek's temperature (*T*) function (from $a = D[T + 9.37]^{2.05}$; see text). Because of the clear anomaly at 15°C in the time between 50% appearance of CV and adult (due possibly to small numbers maturing, and non-separation of sexes), we use times to first appearance at this temperature.

Stages	Interval (d) at 10°C to 50% of stage	Est. *a*	Interval (d) at 15°C to 1st appearance of stage	Est. *a*
CI–CII	4.0	1740	2.9	2020
CII–CIII	2.5	1088	2.9	2020
CIII–CIV	2.7	1175	3.5	2438
CIV–CV	6.3	2741	4.8	3344
CV–Ad.	7.0[a]	3047	3.5	2438

[a]In 2 experiments interval = 7 d; a third took 17 d, which we consider to be abnormally long.

Centropages typicus

Life history

This species is a late-summer and autumn species on Emerald Bank, as elsewhere in the region (e.g. Davis 1987). Life cycles are clear early in the year, when an overwintering population of copepodites and adults in February was followed by a greatly diminished population exclusively of adult females in May (Fig. 8). The low weight of females in February (Table 2) also suggests that they had developed in the warmer waters of the previous autumn. The increase in numbers and appearance of copepodites and adult males in mid-June therefore seem to signal the first new generation of the year. Thereafter, size changes and great increases in numbers suggest that several generations occurred, but times of recruitment cannot be inferred.

Samples from Browns Bank in 1979 show no evidence of stalling or accumulation in younger stages (Fig. 9). Although no clear pattern is evident, the prominence of early stages in August–September, late ones in early October, and early ones again in early November, suggest that at least two generations developed during this interval.

Thus it appears that *C. typicus* had more or less continuous development from late spring through autumn. The enormous increase in numbers in autumn might suggest augmentation from resting eggs. However, Smith and Lane (1987) could not confirm previous suggestions that resting eggs are produced by this species. There is also no indication in our February sample of diapause in a singular copepodite stage. The strong synchrony in spring (i.e. all adult females on 24 May) may have resulted from accumulation in older stages during winter through food shortage or thwarted reproduction.

Smith and Lane (1987) found development from hatching to adult in about a month at 15°C, close to the temperatures on Emerald Bank in late summer and fall when *C. typicus* predominated in our samples. This may help explain why a clear pattern of cohorts is not evident in our variously spaced samples (Fig. 8).

Growth and Reproduction

Dry weights of CIV, CV, and adult *C. typicus* from Emerald Basin varied seasonally (Table 2). The seasonal range of values for adult females (19.6–40.7 μg) is similar to that found by Smith and Lane (1985, 1987) in the New York Bight (range 23.2–41.8 μg). The very large size increments between stages in this species are noteworthy. Mean weight increments, for those samples for which they are available (Table 2), are 87% from CIV to CV, 55% from CV to ad.♂, and 120% from CV to ad.♀ (mean of sexes combined 88%). An even larger mean weight increment of 195% from CV to adult ♀ is found in Smith and Lane (1987; Table 1). Such very large increments are also implicit in the prosome lengths recorded by Lawson and Grice (1970). Ratios of lengths cubed are: CII/CI = 2.24; CIII/CII = 2.28; CIV/CIII = 2.20; CV/CIV = 2.48; ad.♂/CV♂ = 2.09; ad.♀/CV♀ = 2.53.

Information on laboratory development rates of *C. typicus* is deficient. Lawson and Grice (1970) found that embryonic duration was 1.13–1.21 d at 18–19°C, 1.5–2 d at 13–14°C, and >3 d at 8–9°C. The first two estimates (with T taken as 18.5 and 13.5°C, D as 1.17 and 1.75 d, respectively) are implicitly based on more frequent observations than the last one, and can be used to fit Bělehrádek's temperature function (equation (3)), giving $D = 1068(T + 9.37)^{-2.05}$. The fitted temperature-scale correction ($\alpha = -9.37$) is in general agreement with those for other temperate copepods (see McLaren et al. 1986; 1989a). The estimates by Smith and Lane (1985) of 1–2 d at 15°C and ca. 3 d at 10°C are based on daily or less frequent monitoring, but are in rough agreement with those in Grice and Lawson (1970).

To estimate temperature-dependent growth rates we used intervals between copepodite stages at 10 and 15°C from Smith and Lane (1985; 1987). Because these intervals were clearly only roughly determined, we assume equiproportional development and use the above-fitted parameters of Bělehrádek's equation for embryonic duration to estimate the value of a for these stages (Table 5). The increased durations of the two last stages are probably related to greater weight increments in those stages. Instantaneous growth rates are determined from per-stage weight increments for Emerald Bank (see above) and mean values of a (Table 5) as $\ln 1.87/3043(T + 9.37)^{-2.05}$ for CIV and $\ln 1.88/2693(T + 9.37)^{-2.05}$ for CV (sexes combined). We assume that temperature-specific daily growth rates are similar across all copepodite stages (as in some other species; cf. McLaren and Corkett 1981; McLaren 1986). Furthermore, late stage copepodites predominate in the samples (Fig. 8). We therefore apply a mean estimate of daily growth rates (G_i) for CIV–CV and CV-adult, to all copepodites:

$$(5)\quad g_i = \ln 1.88/2868(T + 9.37)^{-2.05};\ G_i = \exp g_i - 1.$$

This yields finite growth rates (Gi) of 10% per day at 10°C and 16% at 15°C. The per-stage growth increments found by Smith and Lane (1987; see above) would give larger values.

Smith and Lane (1987; Table 5) concluded from a variety of experiments that female *C. typicus* produced 1.1–5.5% of their body weight in eggs during the first day of capture. Their estimates of numbers of eggs produced are somewhat lower than those of Razouls (1981). Also, they depend critically upon assumptions that eggs contain 0.018 μg C (thought by them to be low), a ratio of C·dry weight^{-1} of 0.6 (probably high), and that there was no cannibalism (which they state "could underestimate true rates of egg production by as much as 50%"). There is no significant correlation between their estimates of egg matter produced and surface temperatures at time of capture of the females. We feel that a value of 5% per day is very conservative, but use it here.

Production

Numbers are available for adults and ungrouped copepodite stages, although younger ones were clearly undersampled (Fig. 8). Dry weights of CIV-ad. from Emerald Bank (Table 2) were used where possible. Missing weights were estimated using a ratio of 1.88 for both ad./CV and CV/CIV, and earlier stages (CI–CIII) were assumed to double their weights between molts (slightly conservative use of ratios of length^3 under Growth and Reproduction). Unweighed adult ♀♀ on 24 May were taken as 40.1 μg (mean of next two dates) and all stages

TABLE 6. Estimated daily production by *Centropages typicus* on Emerald Bank, 1979–80. Production estimated from temperature (nearest °C) at 14 m (Fig. 2) and biomass of copepodite stages using equation (5), and egg production assumed to be 5% per day in adult females.

	Biomass μg m^{-3}				
Sample date	cop.	ad.♀♀	ad.♂♂	Temp. (°C)	Production (μg·m^{-3}·d^{-1})
26–30 Nov.	2409	1058	788	11	320
19–20 Feb.	30	12	25	3	2
24 May		7		6	0
18 June	24	53	45	11	5
1 Aug.	134	79	45	12	20
25–26 Aug.	976	344	221	14	177
15–16 Sept.	2277	1271	1216	16	473
24–25 Oct.	4099	1266	885	13	707

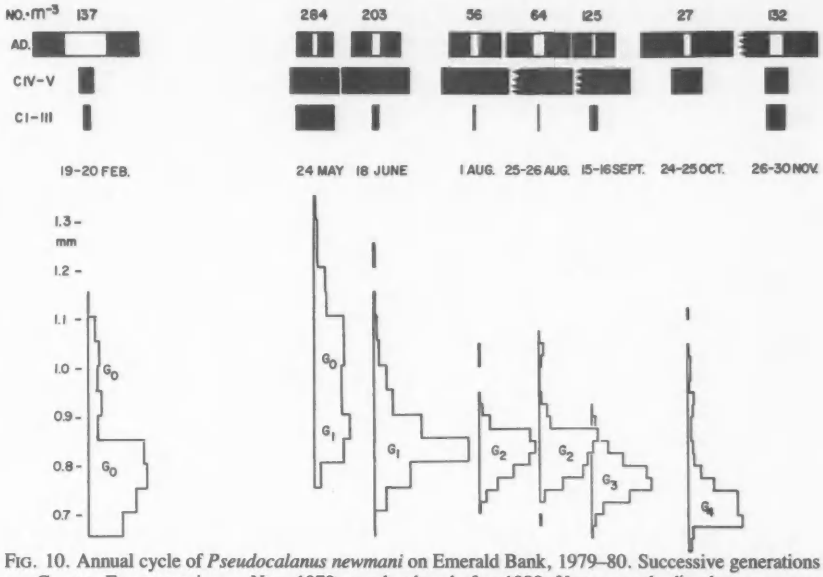

FIG. 10. Annual cycle of *Pseudocalanus newmani* on Emerald Bank, 1979–80. Successive generations are G_0, etc. For convenience, Nov. 1979 sample placed after 1980. Upper panel: abundances as proportions of stages (males clear section of adult bar). Lower panel: size-frequencies of adult females as proportions.

TABLE 7. Weight increments between copepodite stages of *Pseudocalanus* sp. (probably *P. acuspes*) from Halifax, N.S., and *P. elongatus* from the North Sea. After data in Corkett and McLaren (1978).

Temp. (°C)	Increment (%) between stages	
	North Sea	Halifax
0	—	119
3	—	108
6	—	85
8	88	79
10	78	68
12.5	58	60
15	43	—

in October and November, which were not weighed, were assumed to be the same as in September.

Daily production (*PR*) for each sampling period was estimated by equation (2) from combined biomass (B_i) of all copepodite stages and temperature-specific daily growth rate (G_i in equation (5)). To this was added 5% of adult female biomass for egg production (Table 6).

The integrated annual production, using linear interpolation of daily rates (Table 6) between dates, is 63 $mg \cdot m^{-3} \cdot yr^{-1}$. Mean biomass for the year is estimated in the same way as 1856 $\mu g \cdot m^{-3}$, yielding an annual P/B ratio of 34. Although this estimate is based on the assumption that growth rates are uninhibited by food shortages, we have used conservative values for growth increments between stages and for egg production rates.

Pseudocalanus newmani

Life cycles

Past studies of *Pseudocalanus* on the Scotian Shelf have either not discriminated species or referred to them as *P. minutus* (e.g. Tremblay and Roff 1983b). In fact, *P. minutus* (Krøyer) is rarely encountered there and the common species are the newly described (Frost 1989) *P. moultoni* Frost and *P. newmani* Frost (McLaren et al. 1989a). *P. newmani*, which predominates during much of the year over Browns Bank (McLaren et al. 1989a), is smaller (sample mean female prosome lengths 1.0–1.1 mm in spring, 0.8–0.9 mm at other times) than *P. moultoni* (1.1–1.3 mm in spring, 1.0–1.1 mm in summer through winter). On the basis of size, the *Pseudocalanus* over Emerald Bank in 1979–80 were clearly also largely *P. newmani* (Fig. 10).

McLaren et al. (1989a) concluded that *P. newmani* over Browns Bank had at least three generations between spring and autumn, the first two at temperature-dependent intervals. Larger adults of the overwintering generation, G_0, appeared in April–May, G_1 adults in May–June, and G_2 in July–August. They were too scarce in later samples to be certain of subsequent generations, but there was no evidence of "resting" stages.

We believe that five generations matured between spring and late autumn on Emerald Bank (Fig. 10), although the evidence for G_2 is indirect. The first (G_1) was probably largely spawned in early April (as on Browns Bank; McLaren et al. 1989a), its adults recruited largely in mid-June (from size and numerical evidence, Fig. 10). There was no evident increment in numbers or sharp change in size heralding G_2 in summer (Fig. 10). However, adults of G_2 over Browns Bank were quite clearly recruited during late July and early August 1983 and 1984 (McLaren et al. 1989a), and we imply the same for Emerald Bank (Fig. 10). Of subsequent generations, G_3 is inferred from changes in size and numbers to have matured in mid-September, G_4 from size in late October, and G_5 from numbers in late November (Fig. 10).

We could assume, as did McLaren et al. (1989a) from limited data on depth distributions on Browns Bank, that *P. newmani* maintained a depth of ca. 20 m. Then, between spawning of G_0 in early April and maturation of G_5 in late November (ca.

TABLE 8. Assumed generation intervals (nearest half-month), estimated duration of older stages (from proportion of a generation occupied by the period from appearance of CIII to adult), and inferred temperature (nearest °C) during development of *Pseudocalanus newmani* on Emerald Bank (see text for details of calculations).

Generation number	Season	Estimated stage duration (d)	Inferred temperature	Growth per stage (%)
0	30 Nov.–1 April	7.1	4[a]	100
1	1 April–15 June	4.3	4	100
2	15 June–1 Aug.	2.6	6	85
3	1 Aug.–15 Sept.	2.6	6	85
4	15 Sept.–31 Oct.	2.6	6	85
5	31 Oct.–30 Nov.	1.7	10	70

[a]Development slowed below temperature-dependent rate during winter. Temperature is estimated for latter part of this period (when most production occurred) from Fig. 2.

TABLE 9. Estimated daily production rates (biomass, excluding CV♂♂ and ad.♂♂, multiplied by growth per day in percent/100; see text) of *Pseudocalanus newmani* on Emerald Bank, 1979–80. Generation numbers are those of the older copepodites and adults in the samples, although most younger stages may have belonged to the subsequent generation.

Sample date	Generation no.	Biomass ($\mu g \cdot m^{-3}$)		Growth/day (%)	Production ($\mu g \cdot m^{-3} \cdot d^{-1}$)
		cop. + ad.♀♀	CV + ad.♂♂		
26–30 Nov.	5	646	117	37	239
19–20 Feb.	0	877	320	10	88
24 May	0–1	1429	249	13	186
June	1	1233	254	17	210
Aug.	2	336	76	27	91
25–26 Aug.	2	453	81	27	122
15–16 Sept.	3	613	116	27	166
24–25 Oct.	4	166	17	27	45

230 d), at a mean temperature of ca. 8.5°C (from Fig. 2), at temperature-dependent rates (from McLaren et al. 1989b) there should have been 230/(16 356[11.30 + 8.5]$^{-2.05}$) or ca. 6.4 generations, rather than five. Since we cannot be certain of the temperatures experienced by the Emerald Bank population of *P. newmani*, or even if they were developing at temperature-dependent rates, it seems best to use lengths of generations inferred from samples (Fig. 10; see also discussion of Browns Bank samples above) to estimate stage durations, rather than use temperature-dependent development rates. We suggest that G_1 was spawned in early April, G_2 ca. 75 d later in mid-June, G_3 ca. 45 d later in early August, G_4 ca. 45 d later in mid-September, and G_5 ca. 45 d later in late October. The last generation, G_6, is assumed to have been spawned 30 d later in late November, and to have become next year's G_0, spawning 125 d later in early April (Table 8).

Growth and Reproduction

Because only copepodite stages (and largely later ones) are represented in the Emerald Bank samples, all production estimates must be based on growth of these stages. The data themselves (Table 2; Fig. 10) cannot be used to estimate stage-specific growth rates, as CI–III and CIV–V were grouped. Here we justify the use of temperature-dependent growth increments in Corkett and McLaren (1978) for two *Pseudocalanus* species (Table 7), by showing them to have wider validity.

Individual *Pseudocalanus* were removed from a sample taken on Browns Bank on 16 April 1983, when the temperature was about 4°C (McLaren and Corkett 1986; Fig. 3). Dry weights of CV identified as *P. moultoni* averaged 14.1 μg (11.3–18.4 μg, SD = 2.69, n = 6). Lengths of CI were bimodal (0.38–0.41 mm, mode 0.39 mm, and 0.42–0.48 mm, mode 0.45 mm). The larger modal group was taken as *P. moultoni*, and its individuals averaged 2.1 μg (range 0.7–4.7 μg, SD 1.37, n = 8). The implied exponential growth rate per stage is (ln 14.3 − ln 2.1)/4 = 0.48, or ca. 62% weight increment per stage. Other comparable estimates for other species of *Pseudocalanus* can be gleaned from the literature. Davis (1984; Table 1), tabulates weights of CI through CVI in *Pseudocalanus* sp. collected on Georges Bank, giving a mean weight increment of 73% (range 64–100%) between successive stages. Klein Breteler et al. (1982; Table 2) tabulate daily weight increments for CI–CIV and CV females (males growing little if at all) of *Pseudocalanus* sp. (certainly *P. elongatus* per Frost 1989) that average 23.4% per day at 15°C. From their figure 4, a minimal ca. 7 d were required from CI to CV, or 1.75 d per stage. This implies a weight increment of ca. 44% per stage (cf. 43% on Table 7).

The only data available for *P. newmani* are from the rather special environment of Ogac Lake, Baffin Island (McLaren 1969; Table 3; the animals were referred to as *P. minutus*, but according to Frost (1989) are *P. newmani*). During periods of rapid development at temperatures of about 5°C, these increased prosome lengths by an average of 18.7% per stage between CI and CV; females increased by about 20% upon maturity, but males not at all. From the weight–length regression (McLaren 1969; Fig. 8), these length increments imply a mean weight increment per stage (except CV males) of about 88% at this temperature, in excellent agreement with Table 7.

Production

Because temperatures experienced by *P. newmani* are uncertain, we use inferred generation lengths (see above under Life

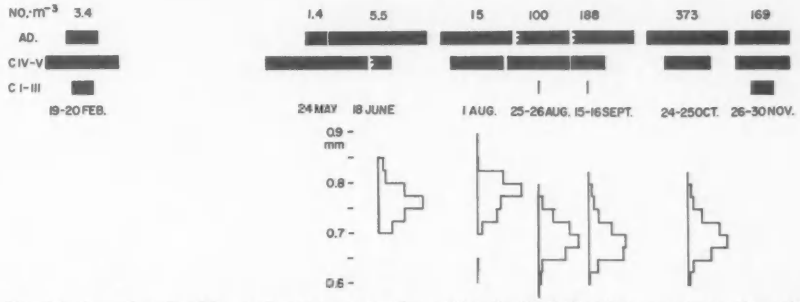

FIG. 11. Annual cycle of *Paracalanus parvus* on Emerald Bank, 1979–80. For convenience, Nov. 1979 sample placed at end. Upper panel: abundances as proportions of stages. Lower panel: size-frequencies of adult females as proportions.

TABLE 10. Weight increments (from Davis 1984; Table 1) and temperature-dependent durations of late stages of *Paracalanus parvus*. The temperature function for embryonic duration (see text) from Checkley (1980; Fig. 2) is used to estimate the values of a, from $D = a(T + 2.97)^{-2.05}$, using stage durations (D) at 15°C (Landry 1983) and 12°C (Davis 1984). (See text.)

Stage interval	Weight increment (%)	Stage duration (d)		Estimated a	
		12°C	15°C	12°C	15°C
CIV–CV	58	2.14	1.74	943	1157
CV–ad.	73	2.14	—	943	—
CV–ad. ♀	—	—	2.38	—	1582
CV–ad. ♂	—	—	1.69	—	1123

cycle) to estimate stage durations during the year (Table 8). Errors in individual generation lengths will tend to cancel out provided our arguments for six generations per year are correct. Mean stage durations are estimated for CIII to CVI (which greatly predominate in the samples; Fig. 10) using data on generation lengths and proportions of total development time occupied by the interval CIII–CVI (estimated as 17% of generation length from McLaren et al. 1989b; Tables 2–4).

Temperatures must be known for accurate estimates of growth increments between stages (Table 7). In the absence of direct knowledge of temperatures experienced by the copepods, they are estimated (Table 8) to the nearest degree celsius from the generation lengths inferred from samples (see under Life cycles), using the temperature function of McLaren et al. (1989b; Table 4). In estimating production rates (Table 9) it is assumed that rate of production of egg matter is the same as weight-specific growth rate in younger stages (as proposed by Corkett and McLaren 1978, p. 131–132), but that adult males and non-growing CV males (assumed to be 25% of the combined counts of CIV–CV) are non-productive. The appropriate biomasses are estimated from Table 2 and the data summarized on Fig. 10. Missing weights of stages on some dates (Table 2) are estimated from mean weight ratios on other dates. Weights for October and November are assumed to be the same as those for the September. Adult males are estimated to weigh the same as CV, from female weights and growth per stage (Table 8). Annual production, from linear interpolation of daily values (Table 9), is ca. 53 $mg \cdot m^{-3}$. Mean annual biomass (all stages, productive and otherwise) is estimated in the same way as 957 $\mu g \cdot m^{-3}$, giving an annual P/B ratio of 55.

TABLE 11. Estimated daily production rates by *Paracalanus parvus* on Emerald Bank, 1979–80. Copepodite production and egg production estimated from temperatures at 16 m (nearest °C from Fig. 2) and female lengths (from Fig. 11) using equation (6) and (7) as explained in text.

Sample date	Biomass ($\mu g \cdot m^{-3}$)		Temp. (°C)	♀♀ length (mm)	Production ($\mu g \cdot m^{-3} \cdot d^{-1}$)
	cop.	ad. ♀♀			
26–30 Nov.	203	382	11	0.68	87
19–20 Feb.	8	7	4	0.76	0
24 May	4	2	6	0.76	0
18 June	3	26	11	0.76	5
1 Aug.	21	58	11	0.77	13
25–26 Aug.	132	274	13	0.68	81
15–16 Sept.	129	736	16	0.68	247
24–25 Oct.	340	1293	13	0.68	320

Paracalanus parvus

Life cycle

Our data on *Paracalanus parvus* come only from Emerald Bank where it is common in late summer and autumn (Fig. 11), as elsewhere in the region (e.g. Davis 1984, 1987). Its annual cycle is not entirely clear in the samples. The coarse nets certainly under-sampled nauplii and younger copepodites. The augmentation of numbers and large size of females in mid-June suggest that they were of the first summer generation. Although female size did not change much on 1 August, numbers swelled and CIV–V became more common relative to adults. The sharp changes in numbers and female size in late August seem clear evidence for recruitment of a further generation. Thereafter, the pattern is unclear; although numbers increased through late October, no major change in female size was evident, possibly because of rather uniform temperatures during that interval (see below). Appearance of younger stages in late November might signal development of another generation.

The effect of temperature (T) on embryonic duration (D_e) has been precisely determined for *P. parvus* off southern California by Checkley (1980), as: $D_e = 482(T + 2.97)^{-2.25}$. Landry (1983; Table 2) estimated the period from egg laying to adult as 16.9 d at 15°C for animals from Washington State, and data in Davis (1984; extrapolation of his figure 2) imply a period from hatching to adult of 29 d at 12°C. If we add a period for embryonic duration to Davis' (1984) estimate, and a further such period for the time between maturation and egg laying (as for *Pseudocalanus*; see Corkett and McLaren 1978), generation

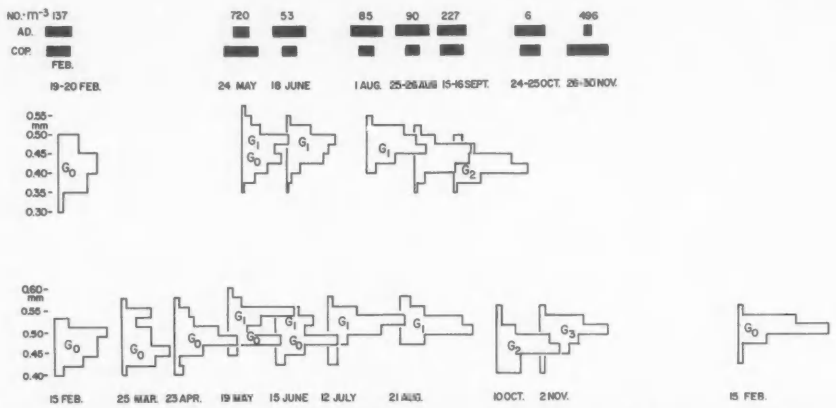

FIG. 12. Annual cycle of *Oithona similis* on Emerald Bank, 1979–80 (upper two panels) and Browns Bank, 1984–85 (lower panel). Successive generations are G_0, etc. For convenience, Nov. 1979 sample placed at end in uppermost panel, which is abundances as proportions of stages (adult males not distinguished). Middle and lower panels: size-frequencies of adult females as proportions.

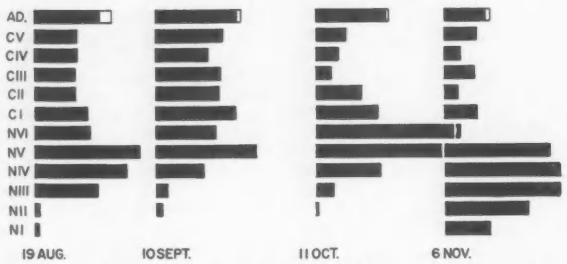

FIG. 13. Relative frequencies of stages of *Oithona similis* in vertical hauls from near bottom (see Table 1) on and near Browns Bank, 1979. Adult males are clear portion of bar.

lengths are 30 d at 12° and 17.5 d at 15°C. As noted by Davis (1984), these are only slightly discordant estimates: using Checkley's (1980) function for embryonic duration yields $a = 30(12 + 2.97)^{2.25} = 13224$, and $17.5(15 + 2.97)^{2.25} = 11635$, respectively. We may take an average value of a to estimate generation length (D) from temperature (T) as: $D = 12430(T + 2.97)^{-2.25}$.

Mean depth of *P. parvus* during late summer and autumn is estimated as 16 m (Table 1). By interpolation from Fig. 2, mean temperature at this depth between late February and mid-June was ca. 4.5°C, implying a generation length of some 135 d. Thus it is plausible that adults in mid-June (Fig. 11) were indeed a first summer generation, spawned in March. Thereafter, temperatures at 16 m (Fig. 2) varied between 10 and 16°C, implying generation lengths of 17–39 d. These frequencies are not discernable in the patterns of numbers and female sizes (Fig. 11).

Growth and Reproduction

Davis (1984; Table 1) tabulates weights of all copepodite stages, implying growth per stage of 61, 24, 78, 58, and 73% during CI–CV, respectively. He lists adult females as 0.74 μm in prosome length and 2.26 μg C. Females on 18 June, 1 August, 25–26 August, and 15–16 September, averaged ca. 0.76, 0.775, 0.69, and 0.69 μm, respectively in prosome length (Fig. 11). For each of these dates, there is a parallel estimate of dry weight (Table 2). By interpolation we estimate that a 0.74 μm female should be ca. 5.9 μg dry weight, 2.6 times the carbon value in Davis (1984, Table 1). This agrees with commonly estimated ratios of dry weight to carbon of ca. 2:1. Thus we feel confident in using growth increments estimated from Davis (1984).

For simplicity the averages of late-copepodite growth increments (66%) and of temperature-corrected stage durations ($a = 1150$) in Table 10 suffice to estimate daily growth rates (G_i) of older copepodites from temperature (T) as

$$(6)\quad g_i = \ln 1.66/1150(T + 2.97)^{-2.25};\ G_i = \exp gi - 1$$

We use Davis's (1984) estimate of egg weight (0.02 μg C × 2.6 = 0.05 μg dry weight) and Checkley's (1980) equation for predicting food-satiated amount of production of egg matter (E) per female from female prosome length (length in millimetres, L) and temperature (T)

$$(7)\quad E = 0.05{\cdot}115{\cdot}(L)^3\,[21/(T + 3)]^{-2.25}.$$

It is of interest to compare growth rate and rate of production of eggs. During August–October when the animals may have experienced average temperatures of ca. 14°C (see below) a copepodite would grow by ca. 29% per day equation (6)). An adult female at this season, ca. 0.69 mm in prosome length (Fig. 11) and weighing ca. 5.5 μg (Table 2) would produce only 1.12/5.5 = ca. 20% of her weight in eggs per day (equation (7)). This mismatch calls for further study.

Production

Because life cycles are not manifest in the samples, we assume, like Davis (1984, 1987), that production by *P. parvus* was temperature-dependent. We use dry weights of adult females from Table 2 (missing weight for May assumed equal to that for February; October and November assumed equal to September). We estimate biomasses of copepodites using numbers combined as CI–III and CIV–V (as on Fig. 11) and their weights relative to those of females in Davis (1984; Table 1); viz., (CI–III)/ad. = 0.16, (CIV–V)/ad. = 0.47). Since the samples are overwhelmingly in the late copepodite stages (Fig. 11), we use equation (6) to estimate daily growth rates from temperatures at 16 m (Fig. 2) and from these biomasses (Table 11), using equation (2).

Adult males were not distinguished in the counts (Fig. 11), but are known to be very short-lived in the field (e.g. Eriksson 1973). Therefore, we assume that all adults were females and estimate the amount of egg matter per female from equation (7), using mean lengths (as on Fig. 11; February–June lengths assumed = to those of 1 August; November = October) and numbers of females (as summarized on Table 11).

Total annual production from Table 11, using linear interpolation between sampling dates, is 27 $mg \cdot m^{-3}$. Mean annual biomass is estimated in the same way as 366 $\mu g \cdot m^{-3}$, giving a very high annual P/B ratio of 74. About 70% is attributable to eggs, so that if egg production were food limited, this would reduce estimates of both production and P/B. On the other hand, copepodites, with higher potential P/B ratios than adult females (from equation (6), (7)), were clearly undersampled (Fig. 11).

Oithona similis

Life cycles

McLaren and Corkett (1986) concluded that *O. similis* on Browns Bank in 1983 had four generations between late February and late October, although temperatures implied that potentially only three should be possible. Data for Browns Bank in 1984–85 (Fig. 12) suggest that three generations occurred during the same period. Females of G_0 were small, although increasing in size through spring with augmentation from overwintering copepodites developing in colder waters. There were distinctly larger size-modes of G_1 females in spring and summer. On Emerald Bank in 1980, the appearance of G_1 seems evident in the sharp increase of numbers and bimodalism in female size on 24 May. The peak of spawning by G_0 on Browns Bank in 1984 might be taken as the time when its female sizes stabilized (i.e. mid-April). Another increase in numbers on Emerald Bank in mid-September, and a drop in female size in both localities, may be interpreted as maturation and spawning of G_2. An increase in female size in early November on Browns Bank can be taken as G_3, and the great increase in numbers of copepodites on Emerald Bank in late November could also be G_3.

The samples taken in 1979 (Fig. 13) can be considered in light of the above analysis. A predominance of nauplii on 19 August followed by an increase in relative abundance of copepodites on 10 September may be the progression of G_2. The peak of later nauplii on 11 October may mark G_3. A strong peak of early nauplii on 6 November may be G_4, spawned somewhat earlier than on Emerald Bank in 1980. Presumably nauplii at this season would form part of an overwintering population, the G_0 of the following spring.

In conclusion, we interpret all these collections as suggesting that G_1 was spawned in about mid-April, G_2 in mid-July, G_3 in mid-September, and G_4 in mid-November, the last entering a long resting or food-limited period to become G_0 of the following year. The inferred generation lengths for G_1, G_2, and G_3 of ca. 90, 60, and 60 d, can be compared with temperature-dependent expectations. Table 1 implies that *O. similis* stayed rather near the surface (mean depth 14 m). Mean temperatures during the above generation intervals in 1984 over Browns Bank at 14–15 m (from McLaren et al. 1989a; Fig. 2) were ca. 6, 11, and 12°C, yielding minimal generation lengths, estimated from McLaren (1978) as $12482(T + 5)^{-2.05}$, of 92, 42, and 37 d. For Emerald Bank during the same periods in 1980, mean temperatures at 14 m (Fig. 2) were ca. 7.5, 13.5, and 13.5°C, yielding generation lengths of 70, 32, and 32 d. Thus, our interpretation indicates that *O. similis* on both banks may have developed more slowly than temperatures would permit during summer–fall. However, much depends on assumed depths and temperatures; developmental temperatures of 8–9°C during summer–fall on Emerald Bank, easily envisaged if the copepods stayed largely below 30 m (Fig. 2), would produce appropriate generation intervals of about 2 mo.

Growth and reproduction

Dry weights of six preserved adult female *O. similis* in a sample from Browns Bank on 16 April 1983 averaged 2.2 µg (range 1.3–3.5 µg, SD = 0.84). This agrees well with the estimate for Emerald Bank of 2.0 ± 0.33 µg (weighted mean and SD for the six samples on Table 2). The weights of CI–CV relative to adult ♀♀ (Table 2) are too high to be representative; earlier copepodites were clearly undersampled.

We turn to the literature for critical weighings of younger stages. McLaren (1969) estimated that volumes of *O. similis* increased by ca. 50% between successive copepodite stages. An independent estimate of weight increments is available from Evans (1977), based on "growth factors" (multiples) of total length and limited weights of preserved animals. This gives values of 61% for stages CI through CV, and 42% for CV to ad.♀. Since values for the last few stages are probably more accurate, and since most animals sampled in the Emerald Bank series were older stages and adult females (Fig. 11), an average value of 50% increase in dry weight between these stages seems reasonable and is used here.

Adult females produce eggs at an unknown rate. Sazhina (1980) indicates that an egg clutch (carried as a double egg sac

TABLE 12. Daily production rates by *Oithona similis* on Emerald Bank, 1979–80. Copepodite and egg production estimated from copepodite biomass equation (8) and female lengths equation (9), using temperatures at 14 m (Fig. 2; nearest °C).

		Biomass ($\mu m \cdot m^{-3}$)		From generation lengths			From temperature	
Sample date	Generation no.	cop.	ad.♀♀	Stage duration (d)	Production ($\mu g \cdot m^{-3} \cdot d^{-1}$)	Temp. (°C)	Stage duration (d)	Production ($\mu g \cdot m^{-3} \cdot d^{-1}$)
26–30 Nov.	3	785	223	4.8	75	11	3.4	108
19–20 Feb.	0	140	169	6.7	7	3	14.1	6
24 May	1	496	381	7.2	36	6	7.4	35
18 June	1	25	86	7.2	3	11	3.4	7
1 Aug.	1–2	42	100	6.0	5	12	3.0	11
25–26 Aug.	2	36	106	4.8	6	14	2.4	13
15–16 Sept.	2	184	352	4.8	26	16	2.0	65
24–25 Oct.	2–3	4	10	4.8	1	13	2.7	1

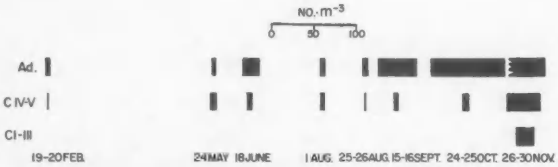

FIG. 14. Numbers of *Clausocalanus* sp. in samples from Emerald Bank, 1979–80. For convenience, Nov. 1979 sample placed at end.

in this species) weighs 21;% of adult female weight. The ratio of temperature-corrected duration of older stages over embryonic duration (i.e. the ratio of a in Bělehrádek's functions) from McLaren (1978) is 1005/1430 = 0.70. Thus, the maximal rate of production of egg matter during an interval between copepodite stages would be ca. $1.21^{0.7} - 1$, or ca. 14% of female weight. Adult males were not distinguished in the samples from Emerald Basin or from Browns Bank in 1984–85 (Fig. 12). However, since they were rare in samples from Browns Bank in 1979 (Fig. 13) and 1983 (McLaren and Corkett 1986; Fig. 4), their non-productivity is ignored in our calculations.

Production

We begin by assuming peak dates of maturation and spawning of successive generations of *O. similis* on Emerald Bank (see above analysis of Life cycles). Assuming (with McLaren 1978) that each generation consists of a period of embryonic development plus 11 isochronal stages, stage duration (Table 12) is estimated as 8% of total generation length (i.e. 8% of ca. 90 d for G_1, 60 d for G_2 and G_3, and 150 d for G_4 ($= G_0$)). Biomasses are estimated from the numerical data summarized on Fig. 12 and from weights on Table 2, applying the mean ratio of weights of (CI–CV)/ad. for February and May to other dates for which only adult weight was taken. Weights for October and November were assumed to be the same as those for September. Production per day (PR_{cop}) can be estimated for copepodite biomass (B_{cop}) from growth per stage (1.5 times) as

$$(8)\quad PR_{cop} = B_{cop}[1.5^{(1/D)} - 1),$$

where D is stage duration in days (Table 12). To this is added an amount per day for female reproduction from adult biomass (B_{ad}; assumed all females)

$$(9)\quad PR_{ad} = B_{ad}[1.14^{(1/D)} - 1).$$

Another approach is to assume that our interpretation of samples is seriously flawed and that stage duration on each sampling date was determined by temperatures at 14 m (from interpolation on Fig. 2), which we tentatively chose as an average depth for *O. similis* in our analysis of life cycles. Under these assumptions, using the temperature (T) function in McLaren (1978), stage durations (D) in days for use in equation (8) and (9) are

$$(10)\quad D = 1005(T + 5)^{-2.05}.$$

These temperature-dependent production estimates sometimes considerably exceed those based on interpretation of life cycles from the samples (Table 12). However, the greatest divergences in estimates generally occur at times of year when biomasses are low.

Total production is estimated from the data on Table 12 (linear interpolation between dates) as 8.4 $mg \cdot m^{-3} \cdot yr^{-1}$ based on life-cycle analysis and 12.3 $mg \cdot m^{-1} \cdot yr^{-1}$ based on assumed temperatures at time of sampling. Mean annual biomass is similarly estimated as 455 $\mu g \cdot m^{-3}$, yielding P/B ratios of ca. 18 and 27, respectively. Tremblay (1981; Appendix 10) gives a larger mean annual biomass of 1115 $\mu g \cdot m^{-3}$ for this small species based on corrections for mesh size of the nets used. Applying the average of our two P/B ratios (ca. 23) to this biomass gives our best estimate of annual production, 26 $mg \cdot m^{-3} \cdot yr^{-1}$, which includes this correction for undersampling.

Clausocalanus sp.

Life cycle

Species of this genus on the Scotian Shelf have been attributed to *C. arcuicornis* (e.g. Herman and Mitchell 1981), but their taxonomy is uncertain and more than one species could be involved. Only limited information is available from the samples of these small animals. Like *Paracalanus parvus* their numbers peak in the warm waters of late summer and autumn (Fig. 14). The proportionately large numbers of adults in June suggest that this was the initial summer generation. Thereafter no pattern is discernable. We assume that like *P. parvus*, *Clausocalanus* may have developed at temperature-dependent rates.

Growth and Reproduction

The only detailed information on growth in this genus appears to be in Sazhina (1980), who reared *C. ingens* from the outer Atlantic shelf off South America. She estimated a daily P/B (including growth and reproduction) of 0.25 for this species at 15°C. This is close to estimates for *P. parvus* at similar temperatures (Table 11; P/B = 0.20 – 0.29 at 13–16°C). Accordingly, we apply the values of P/B implicit for *P. parvus* on Table 11 to *Clausocalanus* sp.

Production

Only one weight of *Clausocalanus* sp. is available (not on Table 2): an average of 7.2 μg (four samples, two stations) for adult ♀♀ on 18 June. As this is close to those for ad. ♀♀ *P. parvus* (Table 2), we assume that similarly grouped stages of *Clausocalanus* sp. (cf. Fig. 11, 14) weigh proportionately the same as for *P. parvus* (see Growth and Reproduction of *P. parvus*). For simplicity we use common values for all dates: 7.2 μg for adults, 3.4 μg for CIV-CV, and 1.2 μg for CI–CIII. This gives biomasses for the sampling periods of November through October (cf. Table 11) of 531, 45, 58, 190, 53, 68, 326, and 631 $\mu g \cdot m^{-3}$, respectively.

Integration after linear interpolation of estimates of sample biomasses and daily production gives an annual production of ca. 14 $mg \cdot m^{-3}$ and a mean biomass of 212 $\mu g \cdot m^{-3}$, for an annual P/B of 66, understandably close to that for *P. parvus* upon which the estimate is largely based.

Calanus hyperboreus

Life cycle

This is the largest copepod in the samples and is clearly annual in life cycle on both Browns Bank and Emerald Bank (Fig. 15). The notable numbers of CIV and CIII in spring virtually disappear in summer, presumably to deeper parts of the shelf or slope. Only a small number of the overwintered generation (G_0) were taken on the banks in spring.

Growth and Reproduction

Females and older copepodites store much lipid, and preserved animals may lose much of this. A single sample of CIV from Emerald Bank on 18 September 1980 weighed 231 μg dry weight·$individual^{-1}$ (corrected for assumed 25% weight

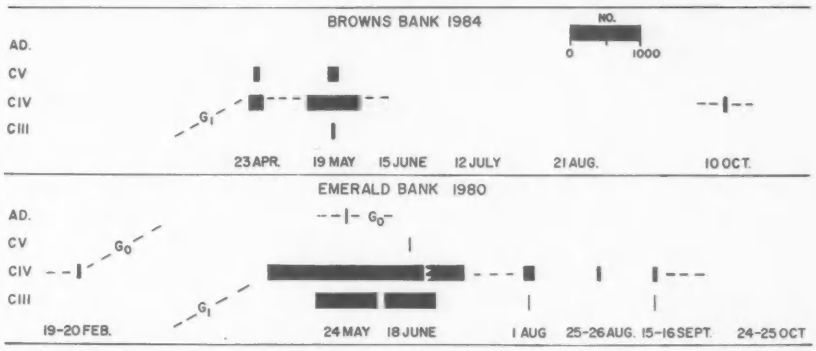

FIG. 15. Annual cycle of *Calanus hyperboreus* on Browns Bank and Emerald Basin. Successive generations are G_0 and G_1. Abundances of stages are No.·100 m^{-3} for Emerald Bank, and No.·haul^{-1} for Browns Bank.

loss). A few individuals from a sample taken from Browns Bank on 19 May 1984 weighed as follows (means ± SE in micrograms, [*n*]; 25% added for preservation loss): ad. ♀, 2690 ± 190 (3); CV, 1054 ± 98 (5); CIV, 298 ± 22 (5). The agreement with CIV from Emerald Bank is quite good. There are few published weight estimates for this species. Total dry weights of 1.4–3.0 mg for females throughout the year in the Arctic Ocean can be inferred from Lee (1974), supporting the plausibility of our estimate of ca. 2.7 mg. From Conover (1964; Fig. 1) it can be estimated that CV's from the Gulf of Maine before starvation in the laboratory averaged 1.77 mg (0.7 mg of which was lipid), much larger than ours. Only Kanaeva (1962) gives (wet) weights of younger stages, from which we estimate a weight ratio CIV/CIII = 3.21. Weight increments in this species, especially between the younger stages, are remarkable and need more study. Using the ratios from Kanaeva (1962) and the dry weight of CIV on Emerald Bank, we apply the following values (micrograms dry weight) in estimating biomasses and production: Ad. = 2700, CV = 1050, CIV = 300, CIII = 93. The important samples were overwhelmingly in CIV's (Fig. 15), which were directly weighed.

Conover (1967) reported that 33 females in the laboratory laid an average of 1340 eggs each, the eggs weighing ca. 1.4 μg dry weight. Many of these were outside the usual breeding season, but nevertheless may reflect average capacity in normal conditions. These eggs may not all add to production, as females produced on average some 450 eggs without feeding (Conover 1967). Such a female weighing 2700 μg (as assumed here) would lose some 630 μg (1.4·450 eggs), which could be readily supplied by lipid stores of ca. 0.6–2.1 mg (Lee 1974; see also Head and Harris 1985). As Conover (1967) found that spent females may weigh only 10% as much as reproductive ones, it may be best to assume that production of egg matter is already accounted for in the large weight increments beyond CIII.

Production

We assume that all production in this species takes place during the brief period of development of copepodites into adults in late winter and of their offspring from egg to late copepodites in spring. We assume that 265 eggs·m^{-3}, each weighing 1.4 μg, were laid about mid-March (based on 1340 eggs each laid by mean of number of ad. ♀♀ on 24 May and 1/2 CIV on 19–20 February) and that these declined exponentially in numbers and grew exponentially in weight to become 30.5·m^{-3} CIII plus CIV averaging 243 μg on 24 May. This yields (from equation (1)) 12.1 mg·m^{-3} in the interval. As for *C. finmarchicus*, this estimate is insensitive to assumptions about initial cohort size; doubling egg numbers yields 14.9 mg·m^{-3}, while halving egg numbers yields 10.1 mg·m^{-3}. If the eggs themselves (here considered as accounted for in copepodite growth) are added to production, they would only contribute 0.4 mg·m^{-3}. To estimate production of the overwintered animals, we use the weight increase from CIV (300 μg) to adult (2700 μg) and the mean number of individuals (0.28·m^{-3}) present as CIV on 19–20 February and as adults on 24 May, giving 0.7 mg·m^{-3}, assumed to have occurred in March. Total production is thus estimated as ca. 13 mg·m^{-3} for the year. Mean annual biomass, from linear interpolation between sample dates, is ca. 1.86 mg·m^{-3}, and annual P/B ratio is ca. 7.

Calanus glacialis

Life cycle

This arctic species is rather rare on Emerald Bank, but of some consequence because of its large size. The samples from Emerald and Browns Banks (Fig. 16) reveal its strictly annual life cycle. Females in late winter produce a G_1 that reaches late copepodite stages in spring, and stays in these stages through summer. The pattern is complicated by the disappearance of almost all G_1 during summer due to their advection off the banks and retention in deeper waters as resting stages. They do not seem to return in large numbers to spawn over the banks in late winter (Fig. 16).

Growth and reproduction

The single available dry weight of *C. glacialis* from Emerald Bank is for CV on 15–16 September (three samples, one station). This estimate, 503 μg, is 3.6 times the average for CV of *C. finmarchicus* (Table 2), and doubtless reflects the very high lipid content of *C. glacialis*. Body volumes of all stages of *C. glacialis* appear to be twice those of *C. finmarchicus* (McLaren et al. 1988), and it is unlikely that structural tissues of the former weigh 3.6 times as much as those of the latter. Nevertheless, their lipid counts as production. Adult females averaged ca. 700 μg in the Greenland Sea (Hirche and Bohrer 1987) and 968 μg dry weight at Spitsbergen (Bamstedt and Tande 1985); the latter give data to estimate weight ratios of ad. ♀/CV = 1.55, CV/CIV = 2.27, CV/CIII = 9.1. We use these ratios, taking CV = 503 μg for the Emerald Bank pop-

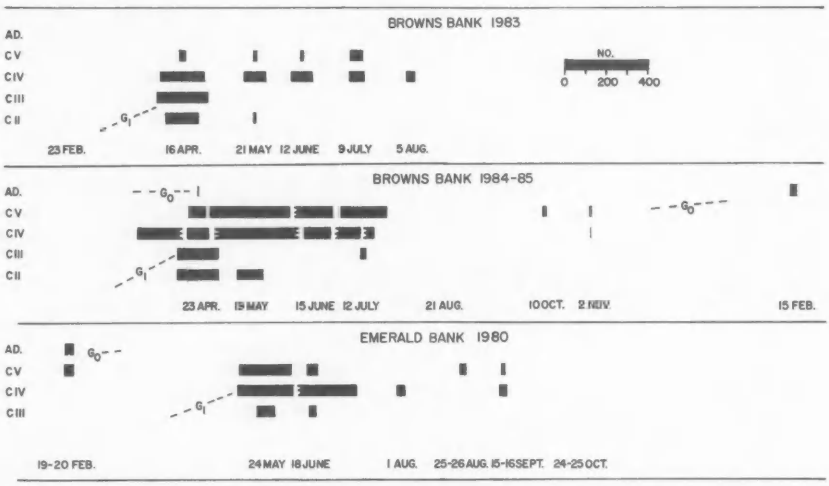

FIG. 16. Relative abundances of stages of *Calanus glacialis* in samples from Browns Bank and Emerald Bank. Bars are No.·100 m^{-3} for Emerald Bank and No.·haul^{-1} for Browns Bank.

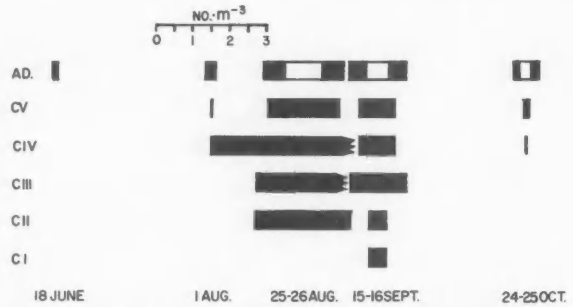

FIG. 17. Numbers of *Candacia armata* in samples from Emerald Bank in 1980. None were found in samples from dates not depicted.

ulation and assuming that adult ♀♀ weigh the same as adult ♂♂.

Hirche and Bohrer (1987) give an egg weight for *C. glacialis* of 0.44 μg C, and assume a carbon/dry weight ratio of 0.43. As their eggs are twice the volume of those of *C. finmarchicus* (McLaren et al. 1988), for which we used a weight of 0.6 μg (see that species), the estimate of 1.0 μg dry weight for eggs of *C. glacialis* is reasonable. We assume that each female *C. glacialis*, like *C. finmarchicus* (see that species), produces 250 eggs during its highly restricted spawning season, and that this represents new production, not utilization of lipid store (see Hirche and Bohrer 1987).

Production

We assume that each female in mid-March (estimated as 0.32 ad.♀♀·m^{-3} and one-half the 0.44 CV·m^{-3} present on 19–20 February) produced 250 eggs, for an initial cohort of 135·m^{-3}, weighing 1 μg each. On 24 May these became ca. 6.0 individuals·m^{-3} with a mean weight of 320 μg (see weights under Growth and Reproduction). Assuming exponential decrease in numbers and increase in weight gives a production of 3866 μg·m^{-3} during the interval, to which 60 μg should be added for growth of females of G_0 and 135 μg for their eggs. This estimate, like those for G_1 of *C. finmarchicus*, is little affected by assumptions about initial size of the cohort. We assume that, thereafter until late winter, no further production occurred (mean sample weight actually decreased on 18 June with relative decrease of CV; see Fig. 16). It is assumed that, after late November, development proceeded from the stage distribution averaged over all dates between 24 May and 15–16 September to the distribution found on 19–20 February (see Fig. 16). We assume that numbers on the latter date were present from the time of renewed development. This yields 380 μg·m^{-3} for the interval. The year's production is then ca. 4 mg·m^{-3}.

Biomass on sampling dates were estimated from numbers summarized on Fig. 16 and the above weights of stages, giving an annual mean, using linear interpolation between sample dates, of 540 μg·m^{-3}. The annual P/B ratio is ca. 8.

Candacia armata

Life cycle

This large, predaceous copepod appeared in numbers on Emerald Bank in summer and virtually disappeared thereafter (Fig. 17). Its episodic appearance may reflect advection of warmer waters onto the Scotian Shelf (Tremblay and Roff 1983a), but could also involve rapid development or a massive hatching of resting eggs. We tentatively suggest that the larger numbers of copepodites on 25–26 August represent the first generation of the year. The peak of CIII on 15–16 September may be of a second generation, perhaps the last, as the population was attenuated by late October. There appear to be no publications detailing life histories of this species or any others of its genus.

Growth and reproduction

The mean dry weight of females in three samples in September was 154 μg. Weights of younger stages were estimated by Tremblay (1981; Appendix 9c) using Robertson's (1968) length–weight regression for *Temora longicornis* as the most appropriately shaped species. These imply a doubling of weight between stages from CI to CV, with a ratio of ad./CV = 4.6. If correct, these estimates imply a very high growth per stage.

Only Bernard (1966) appears to have attempted to rear this species. She found that females produced 19–35 lipid-rich eggs, ca. 0.14 mm in diameter per batch. Hatching occurred within

TABLE 13. Summary of estimated annual production and P/B ratios for major copepod species on Emerald Bank, Scotian Shelf, in 1979–80. Trophic status is herbivore (H), omnivore (O) or carnivore (C). Adult dry weights are averages from Table 2 for the first six species and as given in the text for the others.

Species	Trophic status	Adult dry weight (μg)	Production ($mg \cdot m^{-3} \cdot yr^{-1}$)	Annual P/B
Calanus finmarchicus	H	212	122	8
Metridia lucens	H	107	115	32
Centropages typicus	O	30	63	34
Pseudocalanus newmani	H	10	53	55
Paracalanus parvus	H	6	27	74
Oithona similis	O	2	26	23
Clausocalanus sp.	H	7	14	66
Calanus hyperboreus	H	2700	13	7
Calanus glacialis	H	780	4	8
Candacia armata	C	154	4	34

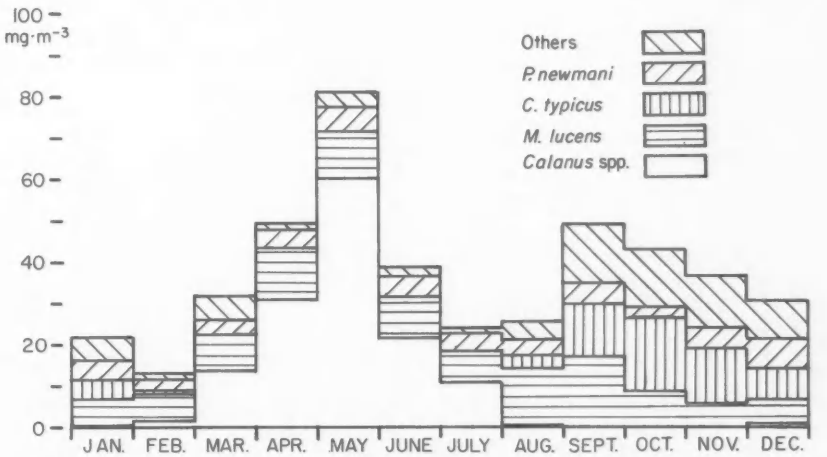

FIG. 18. Estimates of integrated monthly production by copepods on Emerald Bank, 1979–80.

48–60 h at 16.5°C. In the one case of successful development (in enriched medium, but without food), CI was reached in only 6 d. This remarkably rapid early development is thought by Bernard (1966) to be related to the large energy store in the eggs. If this development rate of nauplii were maintained in the early copepodite stages, a growth rate at 16.5°C of 100% per day would be implied. We presume that growth rate is in fact slower, but have no direct evidence on this.

Production

Very tentatively, we assume that the copepodites and adults on 25–26 August were spawned on 1 August, and reached maturity on 15–16 September. In the same manner, we assume that copepodites on 15–16 September represent a new generation spawned on 25–26 August and largely maturing on 24–25 October. We have no insights on total numbers of nauplii initiating the cohorts, but by analogy with *Calanus finmarchicus* (see that species) we suggest 250 eggs per female were produced (or about seven clutches of 35 eggs in *C. armata*), each weighing 0.6 μg (eggs of the two species are similar in diameter).

As with *Calanus finmarchicus*, errors in initial numbers and weights have little effect if we assume exponential growth and exponential decline in numbers from eggs to copepodite stages of the two putative generations. Using this assumption, production by *C. armata* totals 4.2 $mg \cdot m^{-3} \cdot yr^{-1}$. Mean annual biomass is 123 $\mu g \cdot m^{-3}$, and P/B = 34. These estimates are probably less reliable than those for any other species, but clearly *C. armata* contributed very little to annual copepod production.

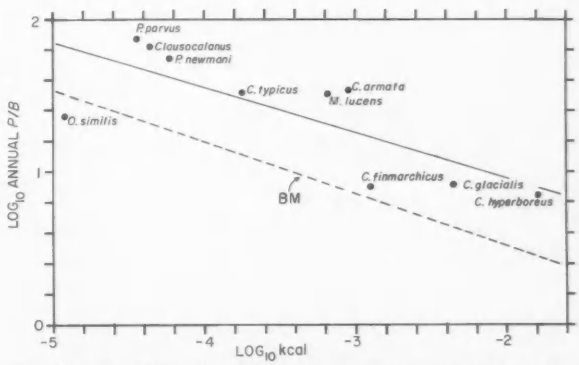

FIG. 19. Annual P/B ratios estimated in the present study ($\log_{10}$ mass in kcal = $0.350 - 0.300 \log_{10}$ P/B, $F_{1,8} = 12.555$, $P = 0.008$) compared with predictions from the mass-dependent relationship proposed by Banse and Mosher (BM regression, $\log_{10}$ P/B = $-0.16 - 0.34 \times \log_{10}$ mass in kcal, after Tremblay and Roff 1983b).

Overall Production

Table 13 lists species in order of estimated annual production. The total, 441 mg dry weight·m^{-3}·yr^{-1}, does not include a few species listed as "others" by Tremblay and Roff (1983b), who estimated that these made up only 0.63% of mean annual biomass. We can express this production as 2.65 kcal or 11.0 kJ·m^{-3}·yr^{-1}, using conversions from Tremblay and Roff (1983b) of ca. 6 kcal or 25 kJ·g^{-1} dry weight. Adopting a mean depth for Emerald Bank of 89.3 m (Tremblay and Roff 1983b) yields estimates of 39 g dry weight, 236 kcal, or 984 kJ·m^{-2}·yr^{-1}. The seasonal distribution of this production is summarized on Fig. 18. Production due to eggs and copepodite growth by *Calanus* spp. was apportioned among months assuming spawning times and exponential growth and survival, as outlined under each species. The monthly estimates for other species were based on linear interpolations between daily estimates on sampling dates. This has the effect of spreading production into months when more or less may have actually occurred. However, the general pattern on Fig. 18 is very clear: a spring period of high production, dominated by *Calanus* spp., is followed by a sharp drop in mid-summer, and a restoration in autumn. Some species, e.g. *M. lucens, P. newmani*, have rather uniform production through much of the year, but others, notably *C. typicus* and *P. parvus* (included in "others" on Fig. 18) flourish in the warm waters of autumn.

Discussion

Our estimates of biomass, production, and P/B ratios are based on few samples from each date, on coarse-mesh nets, and on assumptions and approximations throughout. We could not depend entirely on our own data in our analyses, as much of the sorting, identification, counting, and measuring had been done for other purposes. It is disappointing to find a paucity of published information on such "classical" matters as lengths and weights of subadult stages, so useful for estimating growth rates. The weighing of copepod eggs has only been done for a few species, and we doubt the accuracy of some estimates. A number of species have been reared in the laboratory, but we find no information on such important species as *M. lucens*. Almost as frustrating are published data on some species presented as development rates, sizes, etc., in conditions of excess food, but showing clear signs of inadequate conditions for optimal performance (see discussion of detection of such signs in McLaren et al. 1989a). Further, some species have been reared at only one temperature, thus precluding extension of results to other temperatures. The rule of equiproportional development, which allows use of easily obtained embryonic development rates to predict development rates of older stages from minimal information, has hardly been tried, although it seems well established (e.g. Corkett et al. 1986; McLaren et al. 1989a).

Nevertheless, while neither the absolute estimates nor the relative distributions of production among species and seasons can be taken as very precise, we are confident that they are much the most accurate available to date for any marine locality in eastern Canada.

Our estimate of copepod production on Emerald Bank (236 kcal·m^{-3}·yr^{-1}) considerably exceeds the estimate (530 kJ·m^{-2}·yr^{-1} = ca. 127 kcal·m^{-2}·yr^{-1}) by Tremblay and Roff (1983b), based on the same material analysed here, and also that for herbivorous zooplankton on the Scotian Shelf in general (89 kcal·m^{-2}·yr^{-1}) by Mills and Fournier (1979). Tremblay and Roff (1983b) argued that Mills and Fournier (1979) used an unacceptably low ratio to convert mass to energy (3 kcal·g^{-1}), and suggest doubling this, to give 178 kcal·m^{-2}·yr^{-1}, still lower than ours.

Tremblay and Roff's (1983b) estimates of production were based on a general empirical relationship proposed by Banse and Mosher (1980) for estimating annual P/B ratios from adult body masses ("BM equation"). This approach was criticized by McLaren and Corkett (1984; see also replies by Roff and Tremblay 1984; and Banse 1984) on the grounds that growth and production need not be size-dependent among copepods, and that various aspects of copepod life histories vitiate a general relationship. Nevertheless, the empirical BM equation could account for all such circumstances. Therefore, it is instructive to compare the P/B-size relationship from our analyses with that predicted by the BM equation (Fig. 19). The slopes of the relationships are very similar (fitted regression, $-0.300 + 0.085_{SE}$; taking the BM slope as a single estimate, $t = 0.47$, df 8, n.s.). Ours adds empirical support for interspecific size-dependence of annual P/B ratios among copepods, although the scatter (on a log scale) would limit its usefulness to gross levels of prediction. However, the fitted relationship implies that P/B ratios within the size range of our copepods average 2–2.7 times as large as those predicted by the BM equation (at $\log_{10}$ mass in kcal $= -3.5$, $t = 2.22$, df 8, $P < 0.05$). This agrees with deviations found by Middlebrook and Roff (1986) for *Acartia hudsonica* and *Eurytemora herdmani* in Passamaquoddy Bay, New Brunswick. These deviations underlie the larger overall estimate (ca. two-fold, see above) of production in our analysis compared with that by Tremblay and Roff (1983b). Here we discuss these deviations from levels of production predicted by the BM equation and argue that these cannot in general be attributed to our assumptions that food was not limiting for some species.

The smallest species in our samples, *Oithona similis*, is also the only one in which P/B is below the level predicted by the BM equation, and which departs most from the size-P/B relationship implicit in our comparisons (Fig. 19). Although this cyclopoid copepod is very small there is every indication that it is indeed "slow" compared with small calanoids in life-cycle and metabolic traits. McLaren (1978), concluded from analysis of Marshall's (1949) data that four generations matured between April and September in Loch Striven, Scotland. Digby (1950) thought from sizes and numbers that five generations matured between March–April and October–November off Plymouth, England. The conclusion that three generations matured between May–June and November on the Scotian Shelf is thus comparable. The view of *O. similis* is "slow" as also implicit in the relatively low mass-specific metabolic rate in species of this genus (Lampit and Gamble 1982). The low P/B ratios on Emerald Bank follow from two characteristics of the species. First, it develops relatively slowly at low temperatures (reflected in the value of $\alpha = 5$ in Bělehrádek's temperature function). The annual P/B ratio (Table 12) is actually an average of that based on "observed" generation lengths and that based on the assumption that it lived in warm, near-surface waters through summer. Even if we assume that it was in fact developing at maximal possible rates at these temperatures, its estimated annual P/B would only be 19% higher than this average value. The second feature limiting production rates is the relatively low weight increments between stages in *O. similis* compared with many larger species.

At the other size extreme are the three *Calanus* species. For these we present direct estimates of production from cohort growth, with no assumptions about food or temperature. It may be of interest that production by *C. finmarchicus*, the highest for any species, is quite closely predicted (only ca. 20% too high) by the BM regression. However, it is also important to note that P/B ratios of all three *Calanus* species are very similar. This is because all are basically annual in life cycle and have proportionately similar weight increments, including much lipid, between late copepodite stages. The P/B values for these species could be inflated by the fact that much biomass produced over the bank then disappears into deeper waters. We can probe this effect on P/B for *Calanus hyperboreus* by assuming that, instead of disappearing during summer and autumn, animals stayed over the bank without further growth and declined exponetially from numbers found on 24 May to those found on 19–20 February (see Fig. 15). Then, by integrating between sampling dates, we can estimate a hypothetical mean annual biomass of 2.20 mg, about 18% higher than that actually measured. This would reduce the P/B ratio to ca. 6, still well above prediction (2.8) by the BM equation. The P/B values in this and the other *Calanus* species could still be partly inflated by the failure of populations to return to the bank to spawn in the following spring.

The high values of annual P/B in *P. newmani* and *M. lucens* are largely based on interpretations of life cycles, without any assumptions about effects of food or temperature. We suggested that the latter could have had either three or four generations per year, which would produce P/B ratios some 15% smaller or larger, respectively than the intermediate value shown on Fig. 19. The assumption that both species (laboratory evidence for *Pseudocalanus* spp.) produce egg matter at rates equal to specific growth rates needs to be confirmed by short-term experiments in the manner suggested by Runge (1985). But, even if we assume that *M. lucens*, for example, produced eggs at half this maximal rate, its estimated annual P/B would only be reduced by ca. 20%, still far above the BM prediction.

Finally, there are three species for which, in the absence of clear cohorts in the samples, we were obliged to assume temperature-dependent rates of production. *Centropages typicus* is by far the most important of these, as it is the third highest producer (Table 13). On 1 August, 25–26 August, and 15–16 September, daily production rates (Table 6) were estimated as 7–10%, which might seem excessive. However, during the intervals between these dates, biomass (Table 6) increased at $6\%\cdot d^{-1}$, which does not allow for mortality. Since the population seemed to be turning over rapidly during this period (see shifting female sizes on Fig. 8), we doubt that the population was being inhibited by lack of food to production rates below those determined by temperature. Also, the conservative, temperature-independent rate of production of egg matter used for this species added little to its overall production rate. The temperature-dependent rates used for *P. parvus* are less reliably based, but in this species biomass also increased substantially during its period of prominence (Table 11). Estimates for the remaining species (*Clausocalanus* sp., *Candacia armatus*, the latter not based on temperatures) are quite uncritical, but contribute little.

Finally, it should be reiterated that the general undersampling of biomass of small early stages, would have little effect on biomass estimates and even less effect on annual P/B ratios, since we have argued that mass-specific growth rates differ little among stages within species. Thus we conclude that the high P/B ratios of most copepods in our study compared with those predicted by the BM equation are not a result of systematic errors of sampling or analysis, but reflect realities of production by temperate marine copepods in general.

From the application of species-specific, temperature-dependent growth rates (including some of the rates used here) to the copepods of Georges Bank, Davis (1987) concluded that the seasonal characteristics of the zooplankton cycle in temperate seas has been misconstrued. He believes that the cycle may be largely driven by temperature, so that production in late summer and autumn is of much greater importance than previously supposed. Indeed, estimated production at this season on Georges Bank exceeded that of spring, largely because of *P. parvus* and *Centropages* spp. Although estimated production on Emerald Bank is greater in spring than in late summer and fall (Fig. 18), the resurgence of production in the latter season is dramatic and also largely attributable to *P. parvus* and *Centropages* spp. (*C. hamatus* is common on Georges Bank, rare on Emerald Basin). Although our results parallel Davis's (1987) for Georges Bank, it may be premature to erect general models of the seasonality of zooplankton production in temperate seas. Roff et al. (1988) found that numbers of small copepods off the Northumberland coast in the North Sea peak in midsummer, and that *Calanus* is locally unimportant in spring.

Middlebrook and Roff (1986), assuming temperature-dependent rates, estimated 800–850 $kJ\cdot m^{-2}\cdot yr^{-1}$ for copepod production in Passamaquoddy Bay, only some 16% lower than that for Emerald Bank. Estimated annual copepod production on Georges Bank, is ca. 350 mg $C\cdot m^{-3}\cdot yr^{-1}$, from integration of annual cycle in Davis (1987; Fig. 6). Assuming a C·dry $weight^{-1}$ ratio of ca. 0.5, this is considerably larger than that for Emerald Bank (441 mg dry $weight\cdot m^{-3}\cdot yr^{-1}$). Davis (1987) did not estimate production of *Centropages* spp. from life-cycle interpretations or laboratory rearings, but tentatively used a very conservative daily P/B ratio of 0.1. Our analyses imply somewhat higher values. Since *Centropages* spp. are very important in fall production on Georges Bank, and as the rare species dealt with by us were not considered by Davis (1987), it is probable that annual copepod production on Georges Bank is indeed higher than on Emerald Bank. Nevertheless, given the similarity of life cycles of important species in the two localities, and on Browns Bank as well (this study; see also McLaren and Corkett 1986; McLaren et al. 1989a), it seems that the amounts and seasonal disposition of copepod production may be broadly similar over the whole temperate shelf of eastern North America. A similarity of coastal copepod production over even broader geographic areas was suggested by Middlebrook and Roff (1986). The close agreement between Emerald Bank and the North Sea, where Roff et al. (1988) estimated copepod production at 1260 $kJ\cdot m^{-2}\cdot yr^{-1}$ (cf. 984 kJ on Emerald Bank), supports this view. However, we agree with all these authors that many earlier estimates are suspect, and urge that others carry out the laborious but necessary work required to obtain more reliable estimates of secondary production in the sea. We also suggest that the assumption of temperature-dependence be avoided (or supported) wherever possible by searching for cohorts or by using short-term experiments for direct estimation of rates.

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Benthic Macrofaunal Production of Browns Bank, Northwest Atlantic[1]

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Wildish, D. J., A. J. Wilson, and B. Frost. 1989. Benthic macrofaunal production of Browns Bank, Northwest Atlantic. Can. J. Fish. Aquat. Sci. 46: 584–590.

Benthic macrofauna of the coarse sediments of Browns Bank, off southwest Nova Scotia, Canada were sampled with a modified 0.5-m^2 Van Veen grab; 29 stations from 1983 to 1985. Production was estimated from alcohol-stored biomass by multiplying by the annual turnover ratio, P:B, of each species. The latter was determined from an empirically derived relationship using known or estimated lifespans. Benthic macrofaunal production averaged 64 g wet weight·m^{-2}·yr^{-1} on Browns Bank, markedly lower than the 193 g wet weight·m^{-2}·yr^{-1} in the mixed and finer sediments of the Bay of Fundy. Other community characteristics, such as the number of polychaete and amphipod species for the two areas were similar, which we attribute to the similar geological ages of the sediments. Prey consumed by juvenile age 0 haddock (*Melannogrammus aeglefinus*) consist mostly of deposit-feeding macroinfauna which produce ~1.8×10^4 t wet biomass per year, representing ~8% of the total production of Browns Bank. Two linked hypotheses are proposed to account for the suitability of Banks as juvenile gadid feeding grounds: rapid rates of suspension of macrofauna by strong tidal currents; and drifting animals are of a suitable size and kind for juvenile haddock feeding.

Entre 1983 et 1985, la macrofaune benthique des sédiments grossiers du banc Browns, qui se trouve au large du sud-ouest de la Nouvelle-Écosse au Canada, a été échantillonnée à 29 stations à l'aide d'une benne Van Veen modifiée de capacité 0,5 m^2. La production a été estimée à partir d'une biomasse conservée dans de l'alcool en multipliant le rapport de renouvellement annuel, P :B de chacune des espèces. Ce rapport a été déterminé à partir de la relation empirique de Robertson basée sur des durées de vie connues ou estimées. La production de macrofaune benthique était en moyenne de 64 g·m^{-2}·an^{-1} en poids humide, sur le banc Browns, ce qui est de beaucoup inférieur au 193 g·m^{-2}·an^{-1} des sédiments mélangés et plus fins de la baie de Fundy. Ces deux régions présentent cependant des caractéristiques semblables, notamment le nombre d'espèces de polychètes et d'amphipodes, que nous avons attribuées aux âges géologiques équivalents des sédiments. Les jeunes aiglefins (*Melanogrammus aegle-finus*) d'âge zéro se nourrissent essentiellement de la macro-endofaune déposivore qui produit environ $1,8 \times 10^4$ t par année, en biomasse humide, ce qui représente environ 8 % de la production totale du banc Browns. Les auteurs proposent deux hypothèses reliées pour expliquer pourquoi les bancs conviennent bien comme aires d'alimentation des gadidés juvéniles : 1) la vitesse de suspension de la macrofaune par de puissants courants de marée est rapide; et 2) les animaux en dérive sont de nature et de taille qui conviennent à l'alimentation des jeunes aiglefins.

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A benthic macrofaunal study of Browns Bank, off the southwestern coast of Nova Scotia, Canada, was undertaken as part of a multidisciplinary ecological study of the haddock, *Melanogrammus aeglefinus*, at all stages of its life history in these waters (Mahon and Neilson 1987). In particular, we wished to provide quantitative biomass or production data for benthic communities or species which are prey for haddock during some stages of this fish's life history. Our aim was to undertake comprehensive sampling generally within the 50-fathom contour line of Browns Bank.

Surprisingly little quantitative information on benthic macrofauna at the sediment–water interface is published for the continental shelf of the Atlantic coast off Nova Scotia (see Pocklington and Tremblay 1987). This region stretching from Banquereau Bank in the northeast to Browns Bank in the southwest is referred to as the Scotian Shelf. Apart from studies in inshore coastal areas, the only published work is on soft-sediment infauna (e.g. by Mills and Fournier (1979) and Volckaert (1987) who used a box corer). There appear to be no previous studies of the epifauna or suprabenthos of the Scotian Shelf, particularly of the coarser sediments of which Browns Bank is chiefly composed.

The studies reported here were made with a conventional grab, supplemented with benthic stereophotography. Suprabenthic results obtained in the same area will be presented elsewhere.

Methods

Sampling

During the period 1983–85, nine cruises to the Scotian Shelf were undertaken. Grab sampling results reported here were from six of these cruises and included summer season,

[1]Fisheries Ecology Program Contribution Number: 3

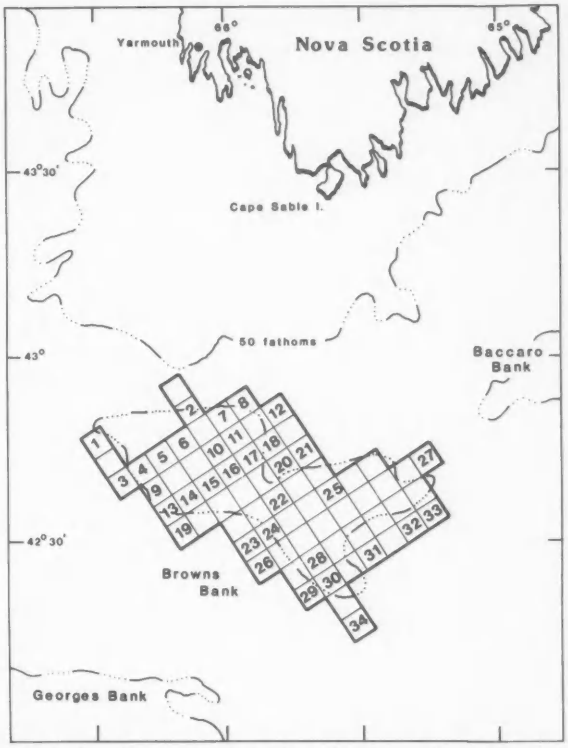

FIG. 1. Sampling area and position of grab sampling stations on Browns Bank superimposed on the 7 × 7 km Greenberg grid.

geographic sampling, temporal sampling at six stations, and underwater stereophotography on five cruises. Sampling was from the research vessels *J. L. Hart* (six cruises), *E. E. Prince* (two cruises) and *C. S. S. Dawson* (one cruise).

Benthic macrofauna was sampled with a 0.5-m^2 Van Veen grab modified according to D. Peer (Bedford Institute of Oceanography, Dartmouth, N.S., pers. comm.) with an overall weight in air of 227 kg and a maximum capacity of 80-L sediment slurry.

A subsample of sediment (~75 mL) was taken from each grab sample and frozen for analysis of sedimentary grain size and a separate 5-mL sample for carbon and nitrogen analysis. The latter was determined in a Perkin Elmer Model 240C analyzer. The remaining sediment was washed and sorted with running seawater on deck through a sieve table having a final square mesh size of 0.8 mm. Macrofauna were washed or picked off the sieves, preserved in 10% formalin in seawater, and stored in sealed plastic buckets. In the laboratory, animals were stained with Eosin-B to enhance visibility, sorted into families or genera and stored in 70% enthanol. These samples were verified by the Atlantic Reference Centre, Huntsman Marine Laboratory, St. Andrews, to the lowest possible taxon. Identified taxa were soaked in water and centrifuged at c. 2000 g for 60 s before weighing to the nearest 1 mg.

Underwater stereophotography was carried out from a separately deployed frame on which two Deepshelf cameras were mounted parallel and downward looking with camera separation to give 60% overlap. Camera height varied from 65–78 cm and photographs were of an area 40 × 40 cm. One or two electronic strobes were mounted at 45° to the camera axis.

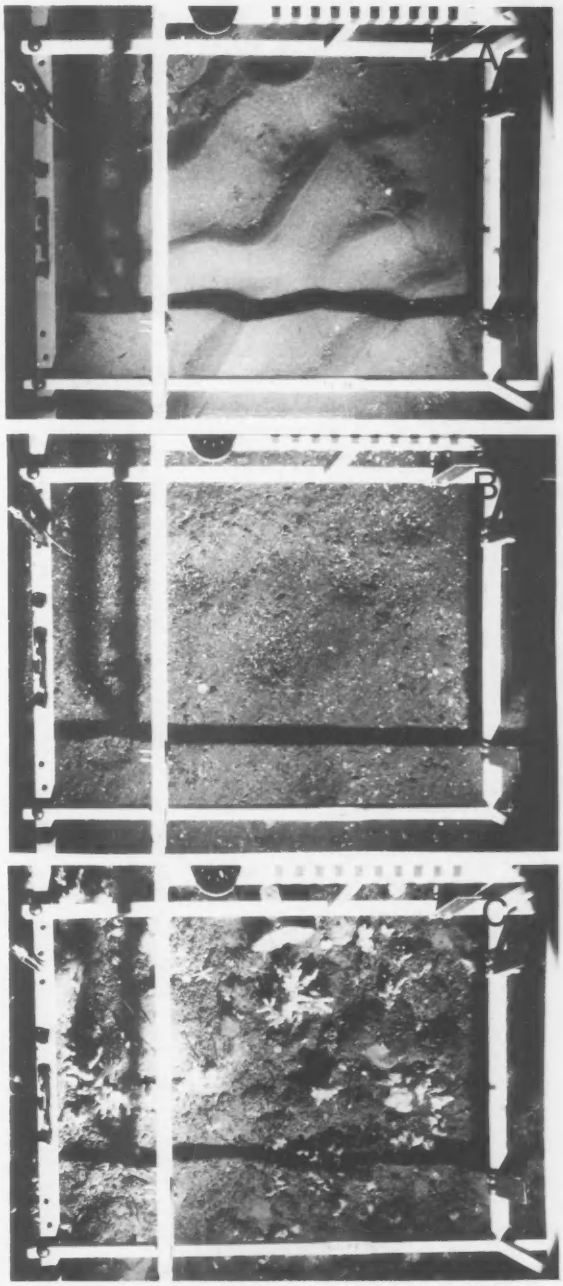

FIG. 2. Underwater photographs taken by Deepshelf cameras in summer 1985. (A) Sambro sand; 9, (B) Sable Island sand; 11a, (C) Sable Island gravel; 11b.

Cameras were loaded with bulk rolls of 35-mm Ektachrome 200 color film and exposures controlled by a programmable microprocessor.

TABLE 1. Benthic sampling stations, total macrobenthic production as g·wet weight·m^{-2}·yr^{-1}, and some environmental parameters for Browns Bank.

Station number	Depth (m)	Volume sampled (L)	Total production g·m^{-2}·yr^{-1}	Sediment				Flow, cm^{-1}·s^{-1}		
				Type	Percent silt/clay	% Carbon	% Nitrogen	Minimum	Median	Maximum
1	110	5.5	66.373	11a	2.57	0.096	0.015	6	43	92
2	62	3.0	16.920	11a	0.73	—	—	10	46	96
3	130	14.0	8.306	9b	2.68	0.082	0.013	6	42	88
4	75	4.5	874.625	11a	—	—	—	6	42	88
5	62	5.0	7.379	11a	1.51	0.041	0.009	6	42	88
6	57	12.0	192.003	11a	0.96	0.033	0.004	10	46	96
7	80	2.0	71.799	11a	—	—	—	10	46	96
8	138	2.0	13.991	9b	—	—	—	7	46	101
9	91	36.0	5.927	11a	2.17	0.041	0.005	6	42	88
10	71	19.0	8.406	11a	1.80	0.077	0.008	10	46	96
11	82	18.0	24.591	11a	2.54	0.040	0.010	10	46	96
13	60	40.0	1.568	11a	0.75	0.049	0.004	8	37	80
14	57	20.0	105.073	11a	1.82	0.061	0.007	8	37	80
15	64	3.0	11.575	11b	1.48	0.053	0.006	10	44	90
16	75	2.0	31.092	11b	—	—	—	10	44	90
17	80	21.0	5.430	11a	2.13	0.048	0.007	10	44	90
18	93	5.0	21.932	11a	9.81	0.100	0.014	9	43	88
19	205	4.0	5.124	?	—	—	—	8	37	80
20	90	28.0	159.110	11b	1.64	0.053	0.008	9	43	88
21	108	18.0	59.111	11b	5.72	0.118	0.020	9	43	88
22	93	0.5	23.941	11b	—	—	—	10	44	90
23	149	10.0	3.695	9a	1.59	0.047	0.006	13	48	95
24	102	53.0	8.818	11a	2.21	0.028	0.010	13	48	95
25	91	2.0	55.763	11b	—	—	—	13	48	95
26	175	26.0	51.951	9b	1.51	0.024	0.006	13	48	95
31	101	0.5	54.695	11b	—	—	—			
32	95	2.0	30.677	11a	—	—	—			
33	102	12.5	16.127	11a	1.54	0.116	0.016			
34	108	9.0	12.578	11a	1.71	—	—			

Analysis

The raw data consisted of species times density or biomass matrices for each of the stations successfully sampled. Density and biomass were expressed per square metre by multiplying the observed values by two. Numbers of species found in each grab were not multiplied in this way but plotted as a function of the actual area sampled (Haedrich 1985). The trophic ratio (*TR*) based on numbers of species of deposit (*D*) and suspension (*S*) feeders,

$$TR = \frac{D}{D+S}\,100$$

was also plotted. Production was determined by multiplying the alcohol wet weight of a species by its P:B (production:biomass) value, summing for all species at each station and expressing as grams per square metre per year. Annual turnover (P:B) rates were determined from the inverse logarithmic relationship of lifespan in years and the annual turnover ratio. Lifespan was estimated or derived from literature sources and P:B empirically derived from Robertson (1979). Each species was categorized trophically as one of the following: suspension-feeding, deposit-feeding, carnivore, omnivore, or other. Productivity charts were prepared by assuming that the single station sampled was representative of the 7 × 7 km area equivalent to the Greenberg (1979) model grid unit in which it occurred. This emphasizes the relatively coarse scale of sampling used in the work reported here.

Originally, it was hoped to compare benthic biological data and tidal data from the corresponding physical model grid unit. However, tidal energy data were available only for each of the 21 × 21 km coarse grid boxes of the Greenberg (1983) model. Output from the model includes a plot of the percentage of time that the depth integrated current exceeds a given flow (centimetres per second) averaged for the year 1978. We determined the median speed of the flow (V_{med}), and the maximum (V_{max}) and minimum (V_{min}) flows.

Results

Physical Conditions on Browns Bank

Of the 34 stations sampled (Fig. 1), satisfactory collections could be obtained from only 29 stations. For the latter, this meant that the grab operated correctly and was retrieved with closed jaws. Nevertheless the penetration efficiency of the grab was variable between stations and the 80-L grab actually sampled from 0.5 to 53.0 L of sediment (Table 1). Coarse, compacted sediments such as occur on Browns Bank are notoriously difficult to sample by grab. Because most of the epi- and in-fauna, which occur near the surface, would be scraped up in the heavy grab, and because there was no positive relationship between volume of sediment sampled and total production (Table 1), we assume that all the stations shown were sampled at least semiquantitatively.

Four surficial sediment types, as described by Fader et al. (1977), were sampled during this study as follows:

9a Sambro sand, <10% gravel,
9b Sambro sand, >10% gravel,
11a Sable Island sand, <50% gravel,
11b Sable Island gravel, <50% sand.

Because quite large stones or rocks were present on Sable Island gravel sediments (Fig. 2c), they were the most difficult to

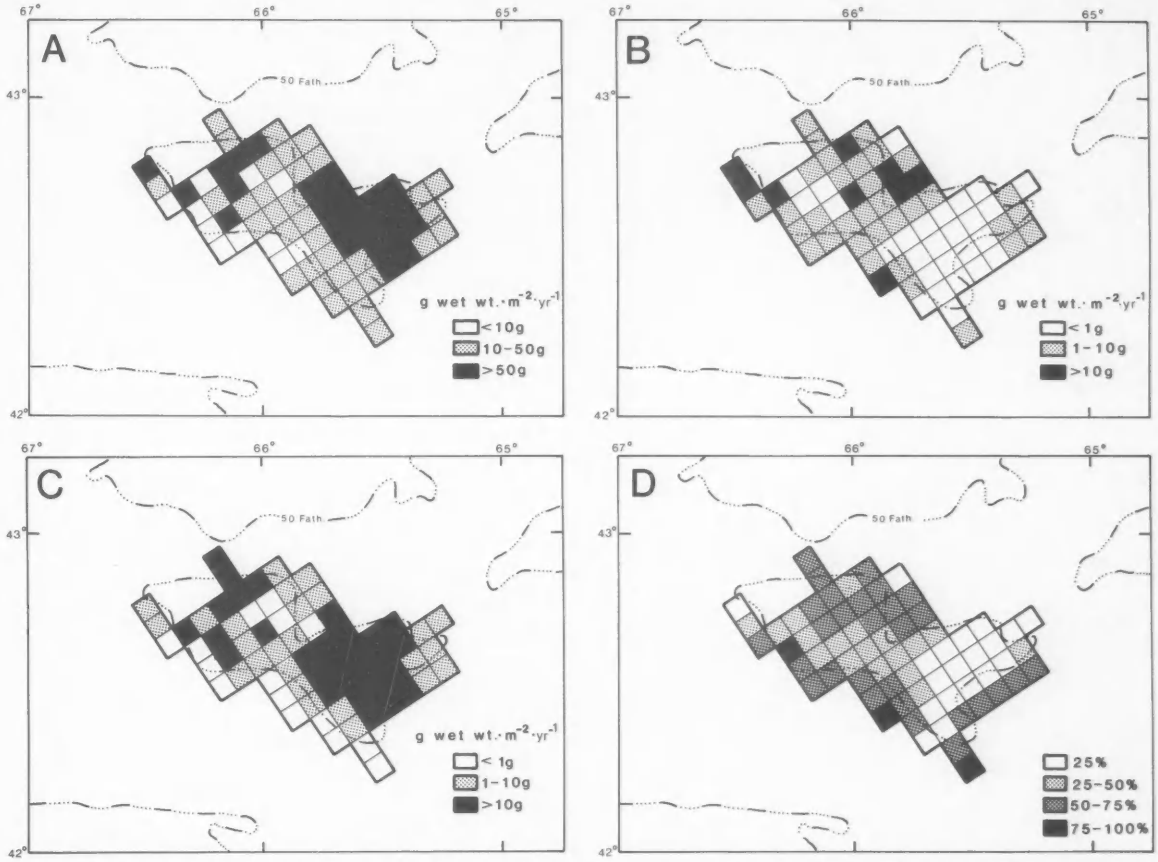

FIG. 3. Distribution of macrobenthic production, (A) total production, (B) suspension feeder production, (C) deposit feeder production, (D) trophic ratio, where $TR = D/D+S \times 100$, D = number of species of deposit-feeders, S = number of species of suspension-feeders.

TABLE 2. Macrofaunal production of Browns Bank estimated from the geographical distribution of 29 sampled boxes, from a total of 69 (See Fig. 1). Each box is 7 × 7 km, hence an area of 3381 km^2.

Trophic group	Calculated mean ($t \cdot km^{-2} \cdot yr^{-1}$)	Annual production ($10^4 t \cdot yr^{-1}$)	Percentage of production
Suspension-feeders	36.78	15.18	88.1
Deposit-feeders	9.16	1.81	11.9
Total	45.94	16.99	100

sample effectively. The five stations that could not be sampled at all were presumed to consist of a rocky bottom.

Eleven of the samples did not provide enough sediment for analysis of carbon and nitrogen because the substrate was too rocky; the remaining 18 determinations yielded an average of 0.062% (range 0.024–0.118%) for carbon and 0.009% (range 0.004–0.020%) for nitrogen (Table 1). One explanation for these low values is that Browns Bank is a net erosional area with high current velocity, up to a maximum predicted flow of 101 $cm \cdot s^{-1}$. In addition, there was no time during the tidal cycle when tidal flows were slack. Thus the sediment samples analyzed were almost always 95–99% sand/gravel with few silt/clay size particles present (Table 1).

Macrobenthic Species and Productivity

From 29 stations on Browns Bank, we obtained 338 taxa identified to species, 100 to genera, and 89 to higher taxon only. Although many of the incompletely diagnosed taxa were probably duplicates of fully identified species, the list is impressively long when compared with Bay of Fundy macrobenthos (Wildish et al. 1986). All identified taxa were used to compute the total production of Browns Bank (Fig. 3A). Based on the distribution of suspension and deposit feeder production (Fig. 3B, C), but excluding other trophic groups, the total production is 16.99 × 10^4 $t \cdot yr^{-1}$ in a surveyed area of 3381 km^2 (Table 2). Over 88% of this production is by suspension-feeding macrofauna. Including all trophic groups, an estimate for overall production is 22.42 × 10^4 $t \cdot yr^{-1}$, of which deposit feeder production represents 8.1%.

Thirty-eight taxa had significant production (i.e. accumulated production >5 g wet $weight \cdot m^{-2} \cdot yr^{-1}$) (Table 3). The majority were suspension feeders and high production is linked to the larger individual size of the higher ranked species.

The distribution of the trophic ratio for Browns Bank (Fig. 3D) illustrates the type of benthic community which is present. The central southeastern portion of the Bank could not be adequately sampled by grab due to the rocky nature of the

TABLE 3. The top 37 taxa ranked by total accumulated production on Browns Bank as g wet weight (*P*). Data arranged in trophic groups with the number of stations (*n*) occupied by each taxon indicated.

Taxa	*n*	*P*
Suspension-feeders		
Cucumaria frondosa	3	563
Potamilla reniformis	8	113
Arctica islandica	1	58
Dendrobeania murrayana	11	50
Cyclocardia borealis	4	45
Ascidia obliqua	1	24
Myxilla incrustans	2	23
Plocamionida ambiqua	2	21
Balanus balanus	2	20
Sertularella tricuspidata	10	17
Tedania suctoria	1	12
Bryozoa	8	12
Caberea ellisii	2	10
Astarte crenata subequilatera	3	8
Sabellidae	8	8
Clavularia modesta	2	8
Parasmittina sp.	1	7
Campanularia verticillata	3	7
Halecium labrosum	2	7
Parasmittina jeffreysi	2	6
Polymastia sp.	5	6
Deposit-feeders		
Echinarachnius parma	13	118
Cerianthus sp.	1	29
Phascolion strombi	11	25
Thelepus cincinnatus	6	18
Maldanidae	22	13
Polychaeta	26	9
Nicomache lumbricalis	2	8
Unciola irrorata	17	6
Carnivores		
Colus stimpsoni	2	177
Alcyonacea	1	127
Nephtyidae	15	8
Colus islandicus	2	7
Nereis zonata	6	7
Omnivorous scavengers		
Foraminifera	11	215
Pagurus acadianus	2	28
Nothria conchylega	8	15

substrate. Underwater photographs taken here showed the sediment to be Sable Island gravels (see Fig. 2c) which were rich in suspension-feeding epifauna. Photographic data were used to help assign *TR* values in this area.

Benthic production was measured on six occasions in the period June 1983 to April 1985 at six separate stations. No obvious trends are apparent in the results for total and deposit feeder production (Table 4), perhaps because the variance associated with repeated sampling of bank areas is so high. As found in the geographic sampling, deposit-feeder production for most stations in Table 4 is a relatively small proportion of the total. For all sampling dates in Table 4, the average deposit feeder production is 8.4% of the total.

The number of species of amphipods and polychaetes for each of the surficial sediment types classified by Fader et al. (1977) is shown in Table 5. The Sambro sand of Browns Bank was not sampled sufficiently to obtain reliable results. All of the $\log_{10}$ species area curves were linear with the exception of polychaetes on Sambro sand in the Bay of Fundy and amphipods on Sable Island sand on Browns Bank, both of which had a single inflection point around 2 m^2 (not shown). Although there were more species of polychaetes than of amphipods, the estimated number of species at 10 m^2 was similar within each taxon in different regions except for Sambro sand in the Bay of Fundy where both polychaete and amphipod species numbers were markedly lower. This is consistent with a low species diversity there caused by limiting current-sediment erosion conditions. In all other regions (Table 5) species number at 10 m^2 was approximately equal. It is of interest that Bay of Fundy and Browns Bank surficial sediments are approximately the same geological age (Fader et al. 1977).

Discussion

Grant and Schwinghamer (1987) have shown that community metabolism of sediments at a 172 m deep station on Browns Bank is relatively low — probably associated with the low input of organic matter received by the sediment from the water column. This is consistent with the relatively low level of deposit feeder production found during the macrobenthic study. As far as benthic production per se is concerned, suspension feeders on Browns Bank are more important because they are adapted to capture organic matter produced elsewhere but transported by tidal flows to them.

The way in which predators utilize benthic production depends on species-specific characteristics. Thus, haddock larvae are visual predators limited to a certain size of prey by their mouth size. Kane (1984) showed that pelagic haddock larvae on Georges Bank consume phytoplankton, copepods, and zooplankters with increasing size selection as the larvae grow. Mahon and Neilson (1987) have suggested that, during the first year of life, juvenile haddock feed in the epipelagic zone until ready to assume demersal life. At this point they make regular vertical migrations to the bottom where they feed. After juveniles have located a suitable bottom, the transition, which takes about 1 mo, becomes permanent and thereafter they feed on benthic prey. These authors also suggested a change in diet as the juveniles increase in size; thus at a body length of <10 cm, 40% of the diet is provided by suprabenthic or pelagic copepods, but at >10 cm body length, only 2–4% consists of this taxon. At this point, the diet consists primarily of benthic amphipod and polychaete macrofauna. The majority of prey items found in the stomach of early benthic haddock juveniles are deposit feeders (e.g. the polychaete *Melinna cristata* and the amphipods *Unciola* spp.) (Mahon and Neilson 1987). Dominant suspension feeding macrofauna contribute little, if anything, to the diet of juvenile haddock (see Table 3). Thus, the prey of juvenile haddock is almost exclusively limited to a trophic group which contributes only ~8% of overall macrofaunal production.

An important question to ask is, why do demersal juvenile haddock find Browns Bank to be a suitable feeding ground? We propose two separate, but linked, hypotheses to account for the fact that Browns Bank, and perhaps banks in general, are suitable as nursery areas for haddock. They are:

— that the rate of physical resuspension of benthic infauna, chiefly motile deposit feeders which lack the specialized attachment adaptations of many suspension feeders, is

TABLE 4. Total macrobenthic production and deposit feeder production (in brackets) as g·wet weight·m^{-2}·yr^{-1} assessed on six separate occasions during 1983–85.

Station	Sampling date: June (1983)	September (1983)	November (1983)	July (1984)	November (1984)	April (1985)	Mean total production	Mean deposit-feeder production	Deposit-feeder production as % of total
5	7.38 (0.14)			120.59 (0.57)	1.03 (0.72)	561.68 (0.48)	172.67	0.5	0.3
3		8.31 (4.55)		35.23 (30.50)	3.97 (0.53)	2.27 (1.16)	12.45	9.2	73.8
11		24.59 (5.98)			252.07 (12.22)	3.76 (2.12)	93.47	6.8	7.3
21		59.11 (18.34)		48.09 (5.69)	21.09 (5.39)	166.66 (8.44)	73.74	9.5	12.8
22		23.94 (5.48)	112.45 (24.27)		10.21 (0.07)	101.60 24.02)	62.05	13.5	21.7
26	51.95 (51.53)		1980.98 (11.51)		90.66 (90.64)	10.92 (5.96)	533.63	39.9	7.5

TABLE 5. Comparison of sampling effort, mean density, species numbers, and individual biomass for polychaetes and amphipods in the Bay of Fundy and on Browns Bank.

Taxa	Number of stations	Surficial sediment	Total area sampled (m^2)	Density as number·m^{-2}	Number of species (S)	Estimated S at sampled area = 10 m^2	Individual wet weight (mg)
Polychaeta							
	Bay of Fundy						
	25	LaHave clay	5.0	122	72	130	64
	25	Scotian Shelf drift	5.0	122	71	120	60
	47	Sambro sand	9.5	60	70	74	49
	97	Total	19.5	92	100	—	58
	Browns Bank						
	24	Sable Island sand	13.5	172	154	130	16
	5	Sambro sand	2.5	142	56	(120)	7
	29	Total	16.0	167	157	—	14
Amphipoda							
	Bay of Fundy						
	25	LaHave clay	5.0	41	25	45	9
	25	Scotian Shelf drift	5.0	73	25	45	9
	47	Sambro sand	9.5	16	19	20	10
	97	Total	19.5	37	37	—	9
	Browns Bank						
	24	Sable Island sand	13.5	86	61	47	2
	5	Sambro sand	2.5	172	12	(55)	1
	29	Total	16.0	108	64	—	2

greater on Banks than elsewhere on the Scotian Shelf and is sufficiently high to support juvenile fish growth, and

— that the resuspended benthic fauna available are of the right individual size and biomass to be suitable prey for juvenile haddock.

To investigate the question of the suitability of banks as a juvenile feeding ground, we compare macrobenthic density and individual size in the Bay of Fundy and on Browns Bank. The Bay of Fundy study involved 97 stations sampled mostly with a 0.1 m^2-grab (Wildish et al. 1986), whereas Browns Bank was sampled during this study at 29 stations with a 0.5 m^2-grab. Because both studies used quantitative techniques, we assume that density, mean biomass per individual and species numbers, expressed as a function of the accumulated areas sampled, will provide a satisfactory basis for comparison. The preferred diet of age 0 demersal haddock consists principally of amphipods and polychaetes (Mahon and Neilson 1987). Lower densities of polychaetes and amphipods occur on the Sambro sands of the Bay of Fundy than on those of Browns Bank (Table 5). It has been suggested previously that the macrobenthic community of Sambro Sand sediments in the Bay of Fundy is an impoverished one with low density and production and low diversity but with some characteristic species that are tolerant of sediment erosion (Wildish 1985). The average density of both polychaetes and amphipods is greater on Browns Bank than in the Bay of Fundy (Table 5); concomitantly, the size of an individual polychaete or amphipod is lower on Browns Bank than in the Bay of Fundy. We noticed that for many species of polychaetes and amphipods, the individuals represented from Browns Bank were smaller and at an earlier growth stage than Fundy individuals; this is consistent with mortality being heavier early in the life history of the Bank population.

Although we can present no direct evidence that the rate of loss of deposit-feeding organisms due to tidal currents is particularly high on Banks, it is a plausible hypothesis. Direct experimental tests utilizing a seawater flume have been undertaken for intertidal amphipods by Grant (1980). He showed that drift of the haustorid amphipods living on a sand flat was density independent, and correlated with darkness and higher flow conditions. Both active and passive drifting were involved in a

phenomenon similar to freshwater invertebrate drifting. It should be possible to repeat this type of flume experiment with typical basin and bank sediments and flows, and hence compare amphipod/polychaete drift rates. Dean (1978) has shown that *Glycera* (bloodworms) swim in the water column at night, which suggests an active component to drifting of some polychaetes. Thus, although deposit feeders form such a low percentage of total benthic production, their suitable size and probable tidal resuspension make the bank environment suitable for juvenile haddock feeding.

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Inter-Annual Distributions of Larval and Pelagic Juvenile Cod (*Gadus morhua*) in Southwestern Nova Scotia determined with two Different Gear Types[1]

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Ichthyoplankton surveys conducted during 1979 on the Scotian Shelf have shown coincident egg and larval distributions for cod (*Gadus morhua*) and other related groundfish species. These data have been used by other investigators to support the larval retention hypothesis, in spite of three limitations: the exclusive use of a single type of small sampling gear, limited sampling landward of the 50-m isobath, and analysis of data collected in a single year. During May of 1985, 1986, and 1987 two gear types were used, from the shelf to coastal waters in southwestern Nova Scotia to assess the horizontal distributions of larval and pelagic juvenile cod. Tucker trawl collections made in each year revealed a cohort of cod ≥10 mm that was not evident in the smaller gear, which effectively sampled cod larvae <10 mm. During 1985 and 1986, when both larvae and juveniles were abundant, their distributions coincided. The mixture of sizes of cod from 3–45 mm reduced the importance of using multiple gear types. The interannual location of young cod shifted markedly between the nearshore and offshore demonstrating that a single year of sampling effort is inadequate to assess their distribution. Nearshore sampling revealed high densities of young cod as much as three-fold greater than offshore. The inshore waters may serve as a nursery area for young cod originating from offshore spawning sites. Our results confirm the existence of two important sampling limitations of previous cod ichthyoplankton surveys that reduce their utility as empirical support for the retention hypothesis.

Des levés d'ichthyoplancton, effectués en 1979 sur le plateau Scotian, ont montré des distributions concordantes d'oeufs et de larves pour la morue (*Gadus morhua*) et autres espèces apparentées de poissons de fond. Ces données ont été utilisées par d'autres chercheurs pour étayer l'hypothèse de rétention des larves, malgré trois limites : 1) l'utilisation exclusive d'un seul type de petit engin d'échantillonnage, 2) un échantillonnage limité du côté terre de l'isobathe de 50 m et 3) l'analyse des données prélevées au cours d'une seule année. En mai 1985, 1986, et 1987, deux types d'engins ont servi à évaluer les distributions horizontales des larves et des jeunes morues pélagiques entre le plateau et les eaux côtières du sud-ouest de la Nouvelle-Écosse. Les échantillons récoltés par le chalut Tucker chaque année ont montré qu'il existait une cohorte de morues de taille supérieure ou égale à 10 mm, dont la présence n'était pas évidente lors des collectes à l'aide du plus petit engin, qui n'a prélevé que des larves de morues inférieures à 10 mm. En 1985 et 1986, lorsque les larves et les jeunes étaient abondants, les distributions ont coincidé. Étant donné que la taille des morues variait de 3–45 mm, il était moins important d'utiliser plusieurs types d'engins. L'aire des jeunes morues a varié de façon marquée entre la région pré-côtière et la région hauturière d'une année à l'autre, montrant qu'un échantillonnage réalisé sur une seule année ne permet pas d'évaluer la distribution. L'échantillonnage réalisé près des côtes a montré la présence de densités élevées de jeunes morues, qui atteignaient trois fois celles des régions plus au large. Les eaux côtières peuvent servir de nourricerie pour les jeunes morues provenant des aires de frai plus au large. Nos résultats montrent bien que l'échantillonnage de larves planctoniques de morues présente deux limites majeures qui en diminuent l'utilité comme résultats empiriques permettant d'étayer l'hypothèse de la rétention.

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The conceptual model of fish migration of Harden Jones (1968) assumes that fish eggs and larvae drift passively from a spawning area to a separate nursery area. However, large-scale ichthyoplankton surveys conducted during the past decade have indicated that several species spawning on either offshore banks or coastal locations produce eggs and larvae which appear to remain within the confines of the spawning area (Gagne and O'Boyle 1984; O'Boyle et al. 1984; Sherman et al. 1984; Koslow et al. 1985; Sinclair and Iles 1988), consistent with the hypothesis of larval retention (Iles and Sinclair

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1982). O'Boyle et al. (1984) showed that distributions of eggs and larvae overlapped for a guild of fishes spawning on the Scotian Shelf, including commercially important gadoids such as cod, haddock (*Melanogrammus aeglefinus*) and pollock (*Pollachius virens*). They argued that these data were indicative of larval retention. Gagne and O'Boyle (1984) concluded that "...over most areas of the Scotian Shelf, cod larvae do not drift from spawning grounds to nursery grounds...instead...are retained in large areas where both types of grounds are located" (p. 514). They suggested that tidally generated gyres occurring over some of the offshore banks may provide a means for retaining eggs and larvae. The limited distribution of cod and haddock larvae within the gyre on Georges Bank also supports the hypothesis of larval retention (Sherman et al. 1984; Smith and Morse 1985).

The conclusions of these recent studies (Gagne and O'Boyle 1984; Koslow et al. 1985; O'Boyle et al. 1984; Sherman et al. 1984; Smith and Morse 1985) should, however, be viewed with caution because of possible biases in the survey design (Cushing 1986; Frank 1988). The foremost limitations are believed to be the exclusive use of a single type of small sampling gear, limited sampling landward of the 50-m isobath, and analysis of data collected in a single year.

The primary sampling gear used in the previous studies was a 61-cm diameter bongo net (333-μm mesh), which cannot provide reliable abundance estimates of the larger, more evasive older larvae and pelagic juveniles (Murphy and Clutter 1972). Cushing (1986) criticized the sampling design of O'Boyle et al. (1984), on the grounds that a spatial separation of eggs, larvae, and pelagic juveniles would have been observed had a larger net been used to sample the larger individuals. For example, haddock eggs and larvae appear to drift from Georges and Browns Banks in a direction consistent with the residual circulation (Colton 1965; Grosslein and Hennemuth 1973), as do lobster larvae originating from Browns Bank (Harding and Trites 1988). The distinguishing feature of the former study was the use of one gear type to sample the egg and larval stages and another to sample the juveniles. An exact analysis of the stage specific distributional patterns during the early life history can only be achieved by sampling the full size (stage) range of the pelagic phase, using both small and large sampling gear. No single sampling device can satisfactorily overcome the dual problems of net avoidance and extrusion (Clutter and Anraku 1968; Green 1979; Cushing 1986; Frank 1988).

The coastal and estuarine environments are often nursery grounds for a variety of 0-group fish, including juvenile cod (Daan 1978; Pihl 1982; Godo and Sunnana 1984; Lear and Wells 1984; Riley and Parnell 1984; MacDonald et al. 1984; Tremblay and Sinclair 1985). Yet many studies of the early life history of gadoids are conducted offshore, with little or no sampling in the coastal (<50 m depth) locations (O'Boyle et al. 1984; Scott 1984; Sherman et al. 1984; Smith and Morse 1985).

The geographic distribution of larvae may vary considerably between years which can have a profound effect on recruitment (e.g. Hjort 1914; Beverton and Lee 1965; Bailey 1981; Cushing 1982). Any conclusions drawn from a single year's survey would be, at best, preliminary (Wiens 1981). The practice of condensing observations from a number of years or even surveys within a year into a single analysis (e.g. Koslow et al. 1985; Sinclair and Iles 1985; Smith and Morse 1985) will also obscure meaningful variability in ichthyoplankton distributions.

We report here on the results of a multi-year survey designed to assess the distribution of larval and pelagic juvenile cod off southwestern Nova Scotia. Two different sized sampling gears were used to sample the early life stages of cod over a sampling grid extending from the offshore spawning area (Browns Bank) to the nearshore zone. The geographic extent of the sampling grid was based on previous biological and physical oceanographic studies conducted in the region (Grosslein and Hennemuth 1973; Smith 1983). We tested the hypothesis that the size and spatial distribution of cod derived from the two types of sampling gear were not significantly different. We also compared the distribution of larvae and early pelagic juveniles between years over the main survey grid. Whether or not significant concentrations of young cod occurred in the shallow (<50 m depth) coastal environment relative to the offshore was assessed from collections made over the main sampling grid and from an additional set of exploratory collections. Finally, we comment on the extent to which each of the suspected sampling limitations has influenced the conclusions of previous studies on the distribution of the early life stages of cod on the Scotian Shelf.

Methods

Study Area

Four young cod surveys were conducted in the spring and early summer of 1985, 1986, and 1987 in the coastal and shelf waters of southwestern Nova Scotia (Table 1). The study area overlapped the southwestern portion of the Scotian Shelf Ichthyoplankton Program sampling grid (O'Boyle et al. 1984), but had approximately twice the station density, and extended farther north from Browns Bank in the direction of the residual current, to include coastal stations at depths <50 m (Fig. 1).

The southwestern Scotian Shelf circulation is dominated by strong semidiurnal tides, particularly over the offshore banks

TABLE 1. Sampling information pertaining to young cod surveys conducted during May of 1985, 1986, and 1987. Range of station distances (from southeastern Browns Bank) and depths are shown. Key to gear deployed: BN, BIONESS; HM, 0.5-m ring; Tt, Tucker trawl.

Cruise	Region	Year	Date	Gear Deployed	Maximum Sampling Depth (m)	No. Stations	Station depth (m)	Distance from Browns Bank (km)
85-1	Browns Bank, and shelf	1985	9–21 May	BN	65	33	40–180	0–167
				Tt	65	29		
86-1	Browns Bank, and shelf	1986	10–18 May	BN	55	34	40–192	9–144
				Tt	55	34		
86-2	Coastal and shelf	1986	14–23 May	HM	15	20	10–110	83–203
				Tt	25	20		
87-1	Browns Bank, and shelf	1987	28 May–4 June	BN	55	56	35–194	9–203
				Tt	40	56		

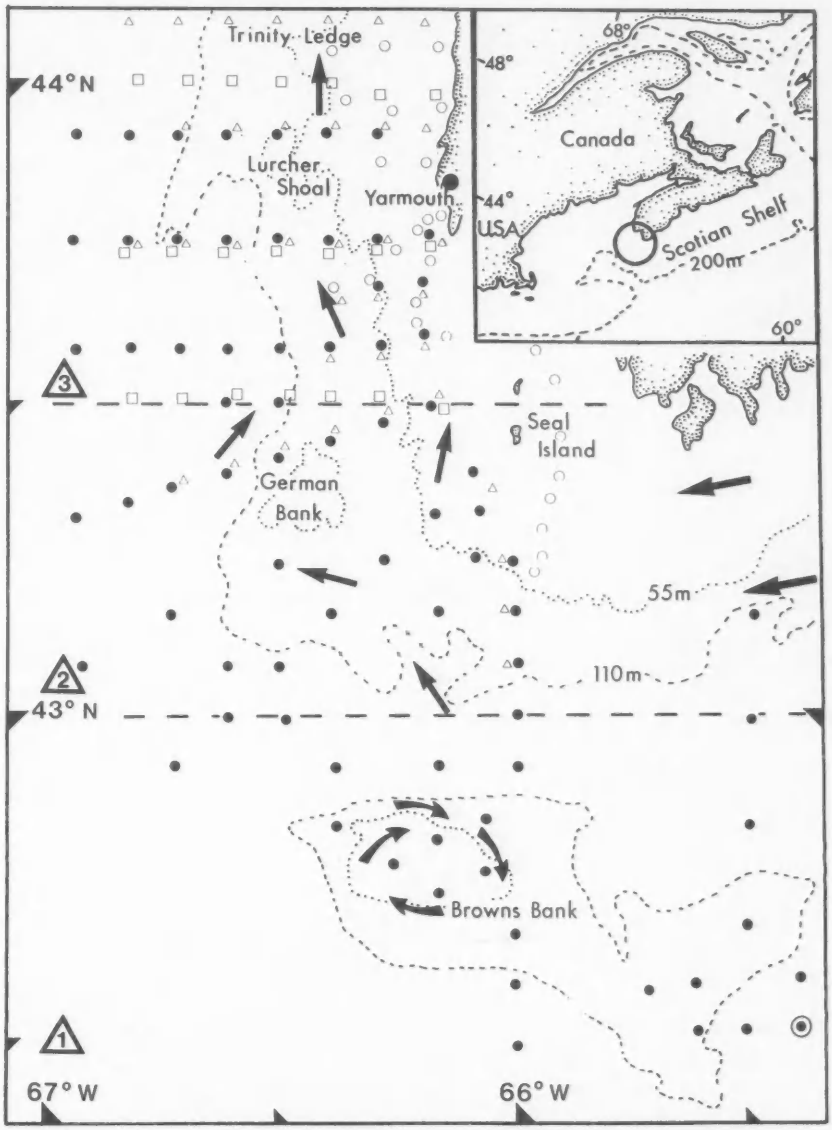

FIG. 1. Stations (closed circles, ●) sampled with small and large gear off southwestern Nova Scotia during May of 1985, 1986, and 1987. Exploratory coastal stations are indicated by open symbols: ○ = 1985, Δ = 1986, □ = 1987. The mean circulation (depicted by arrows) is dominated by an alongshore current of 1–8 km·d^{-1} and a permanent clockwise gyre on Browns Bank (Greenberg 1983; Smith 1983). All catch versus distance relationships examined used the most southeastern station in the grid (circled station) as the origin. Numbered triangles refer to three geographic regions used to further assess the spatial distributions of cod larvae.

where topographic gradients induce eddy formation. The interested reader should consult Smith (1983, 1989) for a detailed description of the hydrographic properties and features of the southwestern Scotian Shelf and Browns Bank region.

Sampling Gear

A 0.25-m^2, 333-μm-mesh mini-BIONESS was used during cruises 85-1, 86-1, and 87-1 (see Frank (1986) for details) and was replaced with a standard 0.5-m diameter, 405-μm mesh ring net on cruise 86-2 (Table 2). The mini-BIONESS recorded temperature, conductivity, depth, pitch, roll, and volume filtered. Temperature and depth were recorded during the 0.5-m ring tows via a conducting cable and towed body that contained the electronic sensors, and volume filtered was recorded with a TSK (Tsurumi-Seiki Co. Ltd.) flow meter.

The two small gear types used during the study were essentially the same with respect to their sampling characteristics. Seven stations sampled with the BIONESS (15–16 May, 158

TABLE 2. Dimensions of the sampling gear used in this study relative to the standard bongo used in previous studies of ichthyoplankton distribution on the Scotian Shelf.

	Mini-BIONESS	0.5-m Ring	Tucker trawl	Bongo
Mouth size (m)	0.5 × 0.5 m	0.5 m diameter	2.5 × 2m	0.61 m diameter
Mouth area (m^2)	0.250	0.196	2.5[a]	0.292
Sample volume (m^3)[b]	1200[c]	250	10 000	350
Mesh size (μm)	333	405	1600	333

[a]Effective mouth opening at 1.5 $m \cdot s^{-1}$ towing speed.
[b]Typical.
[c]Cumulative volume of the seven nets.

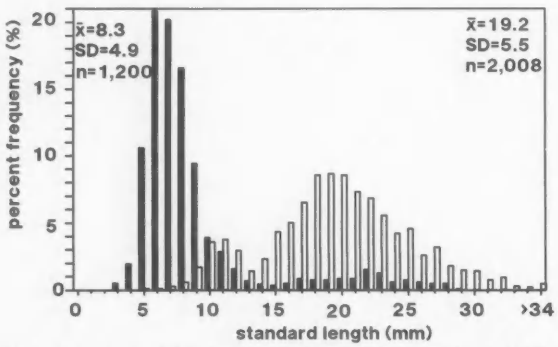

FIG. 2. Composite length frequency distributions of larval and pelagic juvenile cod sampled with the small (shaded bars) and large (Tucker trawl) gear (open bars), respectively during 1985–87.

TABLE 3. Abundance (No.·1000 m^{-3}) and size composition of cod from the small and large gear (Tucker trawl) collections during each cruise period. SL refers to average standard length (in mm).

Cruise	No.	SL	Range	(*n*)	% <10 mm	% ≥10 mm
			Small gear			
85-1	2.10	7.9	2.3–26.5	(104)	83	17
86-1,2	22.02	7.7	3.2–28.0	(1001)	82	18
87-1	0.95	18.2	4.1–29.0	(66)	32	68
			Tucker trawl			
85-1	0.64	20.5	4.1–31.9	(152)	3	97
86-1,2	1.39	17.0	7.5–45.4	(1204)	4	96
87-1	1.28	23.7	15.0–44.0	(577)	0	100

TABLE 4. Spearman rank correlation coefficients between larvae, juveniles, and distance from southeastern Browns Bank for each cruise. All correlations are significant ($p < 0.05$).

	Cruise		
	85-1 (*n*)	86-1,2 (*n*)	87-1 (*n*)
Larvae/juveniles	0.56 (25)	0.34 (54)	—
Larvae/distance	0.69 (33)	0.44 (54)	—
Juveniles/distance	0.85 (31)	0.56 (54)	−0.33 (56)

larvae) were at the same time and area as 10 0.5-m ring samples (17–18 May, 73 larvae) during cruises 86-1 and 86-2. The size distribution of cod larvae from these collections was not significantly different (Kolmogorov Smirnov test, $p > 0.50$; BIONESS: average standard length = 6.9 mm, 0.5-m ring net; average standard length = 7.2 mm). The results of the synoptic cruises 86-1 and 86-2 were therefore combined and hereafter designated as 86-1,2.

A 4.5 m^2-mouth area, 1600-μm mesh Tucker trawl was used to sample larger larvae and pelagic juvenile fishes (Table 2; also see Harding et al. (1987) for details). During cruises 85-1, 86-1, and 87-1 the Tucker trawl was equipped with an electronics package similar to the one on the BIONESS. During cruise 86-2 the Tucker trawl was not electronically equipped, so trawl depth was determined by the length and angle of wire out and subsequently verified with an in situ time-depth recorder. Flow through the net was recorded with a TSK flow meter.

Gear Deployment

The BIONESS sampled seven depth intervals; 5, 10, 20, 30, 35, and where depth permitted, 45 and 55 m (or 65 m), while the 0.5-m ring was towed obliquely from 15 m to the surface. The Tucker trawl sampled two depth intervals in cruise 85-1, 35–5 m and, where possible, 65–35 m. During cruises 86-1 and 87-1 the Tucker trawl was towed between 55 and 5 m, and 45 and 5 m, respectively. During cruise 86-2 the Tucker trawl was simply towed obliquely from 25 m to the surface. Net towing speed for all gear types was approximately 1.5 $m \cdot s^{-1}$.

During cruise 85-1 the entire grid was first sampled with the BIONESS then, starting at the last station, the Tucker trawl sampling commenced and the stations were occupied in reverse order. During cruises 86-1 and 87-1 the large and small gear types were towed consecutively at each station before proceeding to the next station, and during cruise 86-2 the two nets were towed simultaneously at each station.

On deck, immediately following each tow, samples were first passed through a 4- and 10-mm mesh sieve to exclude macrozooplankton (jellies, shrimps, debris), then rinsed into separate containers with freshwater and preserved in 5% formalin, buffered with sodium borate. Most pelagic juvenile cod in the Tucker trawl were transferred to 95% alcohol within 3–10 d of collection to preserve their otoliths.

Exploratory Coastal Surveys

The abundance of larval and pelagic juvenile cod landward of the main sampling grid (Fig. 1) was evaluated during three exploratory cruises: 8–29 May 1985 (30 stations), 5–12 June 1986 (36 stations) and 9–18 May 1987 (18 stations). A 0.5-m (405-μm mesh) and 1.0-m diameter (1000-μm mesh) ring net were used to make the collections. A Tucker trawl was used in addition to the 0.5-m ring net during June 1986. The gear was deployed in a manner identical to that previously described.

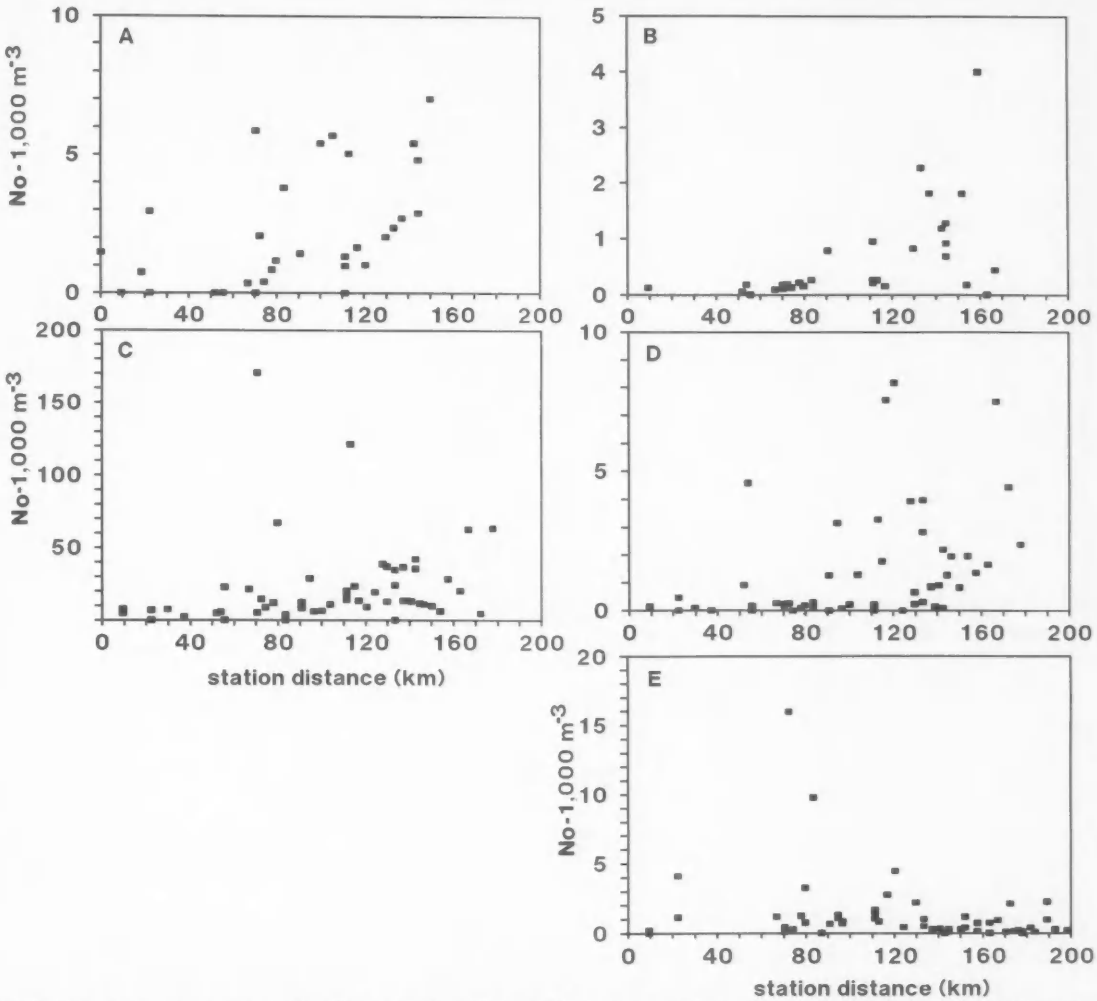

FIG. 3. Relationship between concentration of larvae and juveniles and distance from southeastern Browns Bank during cruise 85-1 for (A) larvae and (B) juveniles, 86-1,2 for (C) larvae and (D) juveniles and 87-1 for (E) juveniles. Spearman rank correlation coefficients in Table 4.

Analysis

All cod were counted and standard lengths of larvae measured to the nearest 0.1 mm using an ocular micrometer. Standard lengths of juveniles were measured to the nearest 0.5 mm using a ruler. No length corrections were made for preservation shrinkage. Cod densities were expressed as individuals·1000 m^{-3}. Abundance of cod larvae at each station estimated from the BIONESS was calculated as a weighted average concentration (i.e. the total number collected at each station was divided by the total volume filtered over the seven depth strata). The Tucker trawl collections were treated similarly when more than one depth stratum was sampled per station.

The distribution of cod larvae and juveniles was assessed during each survey by rank correlation analysis. The relationship between larval and juvenile cod density and distance from the most southeastern station sampled (Fig. 1) was also assessed using rank correlation methods. This location is within the vicinity of major offshore spawning concentrations of cod (Scott 1983; O'Boyle et al. 1984), it was assumed to represent the origin of cod eggs in our study, and distance–density relationships were deemed useful for interpreting inter-annual variability in distribution.

The sampling grid was broken down into three transverse regions (Fig. 1) in order to assess inter-regional differences in the abundance and size composition of cod collected from the two gear types. Region 1 included Browns Bank (the principal late winter–early spring cod spawning grounds in the area). Both regions 2 and 3 contained several nearshore stations at depths less than 50 m (Fig. 1). Mann-Whitney U tests were used to make multiple comparisons of cod densities between regions (1–2, 2–3, 3–1). A similar set of comparisons were made on the length frequency distributions using the Kolmogorov-Smirnov test. Significance levels for these tests were adjusted to comply for multiple comparisons (Steele and Torrie 1980). All statistical analyses were performed using SYSTAT 3.0 (Systat Inc. 1984, Evanston, Illinois).

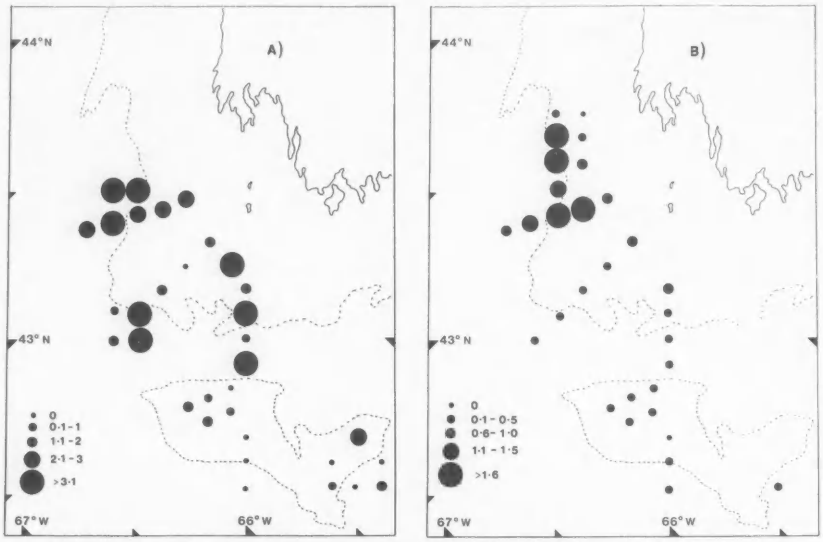

FIG. 4. Expanding symbol plot of cod concentration (No.·1000 m^{-3}) during cruise 85-1. (A) cod larvae sampled with small gear and (B) pelagic juveniles sampled with the Tucker trawl. Note five extra stations were sampled on Browns Bank with the BIONESS, and seven extra stations were sampled at the northern boundary of the grid with the Tucker trawl.

TABLE 5. (a) Regional summary of average cod densities (No.·1000 m^{-3}) from the small and large (Tucker trawl) gear types for each cruise. *n* refers to number of stations sampled and percentage shows regional breakdown of mean catch. (b) Probability values of Mann-Whitney U test comparing cod concentrations between regions sampled by the small gear (SG) and the Tucker trawl (Tt). Insufficient data for analysis (I).

		Small gear			Tucker trawl		
Cruise	Region	No.	*n*	%	No.	*n*	%
(a) 85-1	3	5.90	(2)	62	1.23	(7)	59
	2	2.66	(16)	28	0.76	(13)	36
	1	0.99	(15)	10	0.11	(11)	5
86-1,2	3	24.61	(11)	36	2.45	(11)	53
	2	20.37	(28)	30	1.17	(28)	25
	1	23.21	(15)	34	1.04	(15)	22
87-1	3	I			0.53	(21)	13
	2	I			1.31	(21)	31
	1	I			2.35	(14)	56

Cruise	Gear	Region 1–2	Region 2–3	Region 3–1
(b) 85-1	SG	0.01[a]	I	I
	Tt	<0.01[a]	0.66	0.02[a]
86-1,2	SG	0.17	0.55	0.14
	Tt	0.44	0.02[a]	0.01[a]
87-1	Tt	0.95	0.02[a]	0.13

[a]Statistically significant difference.

Results

I. *Gear Comparison*

More than 80% of the catch with the small gear during 1985, 1986, and 1987 was less than 10 mm (Fig. 2). The grand mean and range of the size distribution was 8.3 mm and 3–29 mm, respectively. The range in sizes was quite broad during each of the surveys in all 3 yr (Table 3). Standard lengths averaged 7.9 and 7.7 mm for cruises 85-1 and 86-1,2, respectively, in spite of a nearly 10-fold greater density of young cod witnessed during cruise 86-1,2 (Table 3). During cruise 87-1 (conducted later than the other cruises by 3 wk) there were very few cod larvae and relatively more cod >10 mm collected. This resulted in a greater average length (18.2 mm) and a lower percentage of larvae <10 mm (32%).

The Tucker trawl consistently caught large cod larvae and pelagic juveniles that were evident only infrequently in the small gear samples. Greater than 95% of the Tucker trawl catch was composed of cod ≥10 mm (Fig. 2). The grand mean and range of the size distribution was 19.2 mm and 4–41 mm, respectively. The average length of cod collected during the 1985 and 1986 cruises was quite similar (85-1; 19.0 mm, 86-1,2; 17.7 mm) whereas during cruise 87-1 the mean was 23.7 mm. Cod larvae <10 mm made up less than 4% of the catch during each of the cruises over the 3-yr period.

Overall, there were at least two cohorts of cod in the study area, one comprising larvae between 4 and 10 mm and the other composed of late larval and early pelagic juveniles >10 mm (Fig. 2). In all cruises, the small sampling gear occasionally caught large larvae while the Tucker trawl occasionally caught small larvae. In the following analyses we define "larvae" as those cod sampled by the BIONESS and 0.5-m ring net, of which >80% were <10 mm. "Juveniles" are defined as those individuals, both large larvae and pelagic juveniles (after the definitions of Hardy (1978), Fahay (1983), and Kendall et al. (1984)), sampled by the Tucker trawl, greater than 95% of which were ≥10 mm.

The abundance of cod larvae <10 mm collected in the small gear always exceeded the large gear catch, on average, by one to two orders of magnitude ($p < 0.001$). This difference can be attributed to the extrusion of small larvae (<8 mm) through

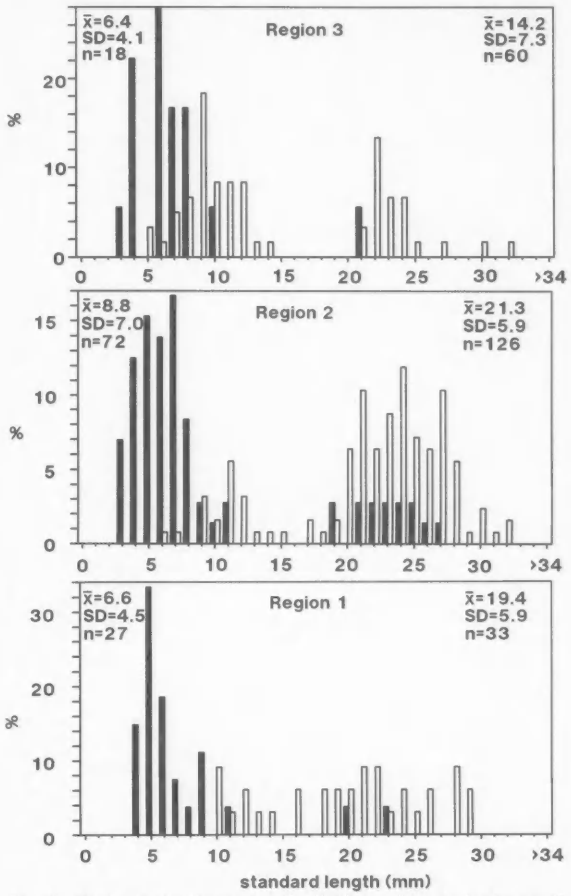

FIG. 5. Regional size frequency distributions of larvae in the small gear (shaded bars) and pelagic juveniles in the Tucker trawl (open bars) during May 1985 (cruise 85-1). Probability values associated with Kolmogorov Smirnov comparisons of length frequency distributions between regions for small gear: region 1,2; 0.99. Tucker trawl; region 1,2; 0.91, region 2,3; 0.01*, region 3,1; 0.08. * - refers to occurrence of statistically significant differences.

the 1600-μm mesh of the Tucker trawl. Conversely, the density of young cod >10 mm was significantly greater in the Tucker trawl ($p = 0.025$, Mann-Whitney test). The frequency of zero catches of cod ≥10 mm exceeded 50% among those stations sampled with the small gear compared with only 17% with the Tucker trawl.

II. *Intra- and Inter-Annual Distribution*

The horizontal distribution of larval and juvenile cod coincided during cruises 85-1 and 86-1,2, as indicated by the significant ($p < 0.05$) positive correlations between their relative abundances at each station and similar positive correlations with distance (Fig. 3, Table 4). During cruise 87-1, too few larvae were collected for statistical analysis although juveniles were abundant. In contrast to the results obtained in the May cruises of 1985 and 1986, pelagic juveniles were negatively correlated with distance from Browns Bank (Fig. 3).

Cruise 85-1

Cod larvae and juveniles were distributed to the northwest of Browns Bank during May 1985 (Fig. 4). Only 10% of the total mean catch of larvae and 5% of the total mean catch of juveniles were collected in the vicinity of the bank (region 1). The density of cod larvae and juveniles increased from region 1–3 such that 62% of the larvae and 59% of the juveniles occurred in region 3 (Table 5) (i.e. at stations in excess of 145 km from the bank). Mann-Whitney U comparisons of larval cod densities revealed significant differences between region 1 and region 2 (Table 5). Only two stations were sampled in region 3 therefore no density comparisons were made with the other regions. Juvenile densities in regions 2 and 3 were not significantly different, but both were different from region 1 (Table 5).

There was no simple trend in the average length of cod larvae and juveniles across the three regions (Fig. 5). Significant differences in the juvenile size frequency distributions existed between regions 2 and 3. The difference in average size of larvae between regions was less than 3 mm and for juveniles it was 7 mm (Fig. 5). The high proportion of small cod (5–15 mm) in the large gear collections in region 3 was peculiar, given the great distance from Browns Bank. The exploratory coastal survey conducted in region 3 did, however, reveal large pelagic juveniles in the 20–30 mm size range (I. M. Suthers, unpubl. data).

Cruise 86-1,2

The larvae were uniformly distributed across the three regions during May 1986 (Fig. 6), and no significant differences in the abundance of larvae was observed between regions (Table 5). The size frequency distributions of larvae were also similar between regions (Fig. 7) with a regional difference in average length of 1.2 mm.

The abundance of juveniles increased from region 1–3 (Fig. 6), an observation consistent with the results from cruise 85-1 (Table 5). Region 3 yielded 53% of the total mean catch and the abundance of juveniles in this region differed significantly from the other two (Table 5). The differences in the average size of juveniles between regions was less than 0.5 mm, and no length frequency distributions were significantly different (Fig. 7).

Cruise 87-1

Too few larvae were collected in 1987 for any meaningful analysis. Juveniles were abundant however, especially in region 1 where 56% of the total mean catch occurred. Abundance decreased from regions 1–3 (Table 5). This trend was opposite to that seen in the previous surveys. Only regions 2 and 3 showed significant differences in abundance which is a surprising result given the regional catch distribution (Fig. 8). Equal ranking of a few high catches in region 1 with those in region 3 explains this result. The juvenile size frequency distributions between region 1 and the other two regions were significantly different (Fig. 9). The difference in average length between regions 1 and 3 was less than 3 mm.

III. *Coastal Distribution*

Several coastal stations were occupied during the main grid sampling. In addition, exploratory coastal surveys were conducted in May 1985, June 1986, and May 1987. Collectively,

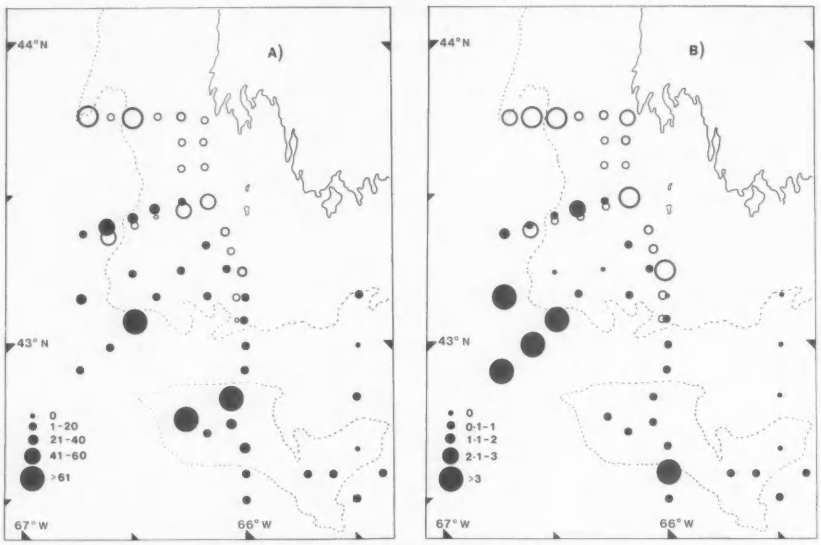

FIG. 6. Expanding symbol plot of cod concentration (No.·1000 m^{-3}) during cruise 86-1 (closed symbol) and cruise 86-2 (open symbol) for (A) cod larvae and (B) pelagic juveniles.

these surveys revealed significant concentrations of larval and pelagic juvenile cod that in some years were greater than in adjacent deeper water (Fig. 10). During May 1985 the coastal abundance of larval and pelagic juvenile cod was three-fold greater than in offshore areas.

Discussion

Any interpretation of larval fish distributions, and inferences regarding the processes underlying larval drift and retention require unbiased estimates of size and abundance. We addressed these requirements by (1) using multiple gear types, (2) examining inter-annual variability over a 3-yr period, and (3) sampling a grid of stations that encompassed the spawning areas and the most probable drift trajectory.

One important result of our study was that each gear effectively sampled only one of two size categories of cod with no one gear being adequate over the full size range. Reliable abundance estimates of cod <10 mm and ≥10 mm were obtained by the small and large gear, respectively. Another important finding was the annual occurrence of significant concentrations of cod larvae and juveniles in the nearshore (<50 m) waters off southwestern Nova Scotia suggesting that the coastal region may serve as an important nursery area for cod. The restricted size range of cod available to the small gear, coupled with limited sampling in the coastal regions, suggests that previous data generated in this way used to analyse the dispersal of the early life stages of cod (Gagne and O'Boyle 1984; O'Boyle et al. 1984) was not representative of the true distribution.

Our null hypothesis that the spatial distributions of cod from the large and small sampling gear would be similar could not be rejected. Although the large and small gear captured different sizes of fish, the positive correlations between cod larvae and juveniles witnessed during 1985 and 1986 supports the null hypothesis. Apparently this is due to the lack of any gradient in size from offshore to nearshore (Fig. 5, 7, and 9). Instead we observed a mixture of sizes during each survey. The length

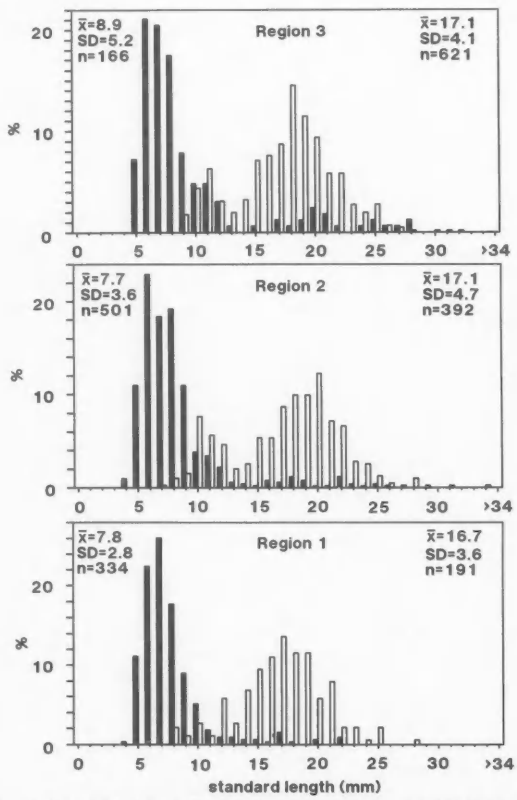

FIG. 7. Regional size frequency distributions of larvae (shaded bars) and pelagic juveniles (open bars) sampled during May 1986 (cruise 86-1,2). Probability values for K.S. comparisons for small gear: region 1,2; 0.99, region 2,3; 0.44, region 3,1; 0.99. Tucker trawl: region 1,2; 0.23, region 2,3; 0.99; region 3,1; 0.39.

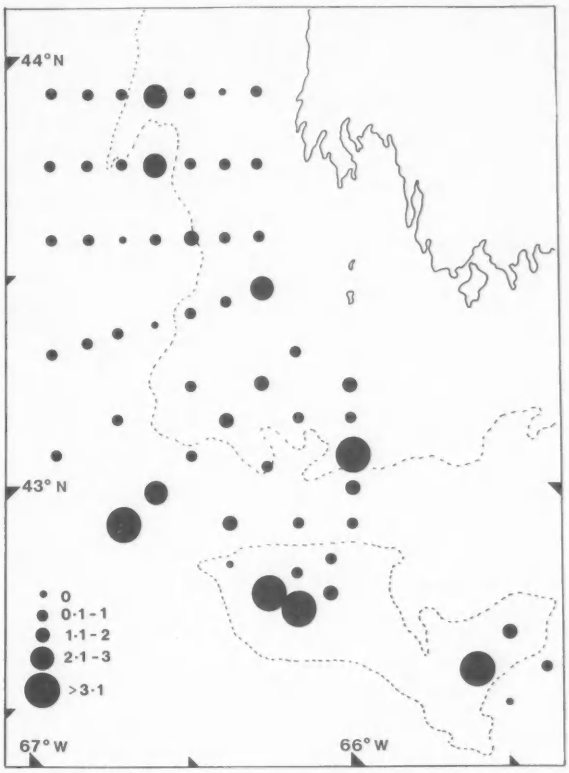

FIG. 8. Expanding symbol plot of pelagic juvenile cod density (No.·1000 m^{-3}) sampled during cruise 87-1.

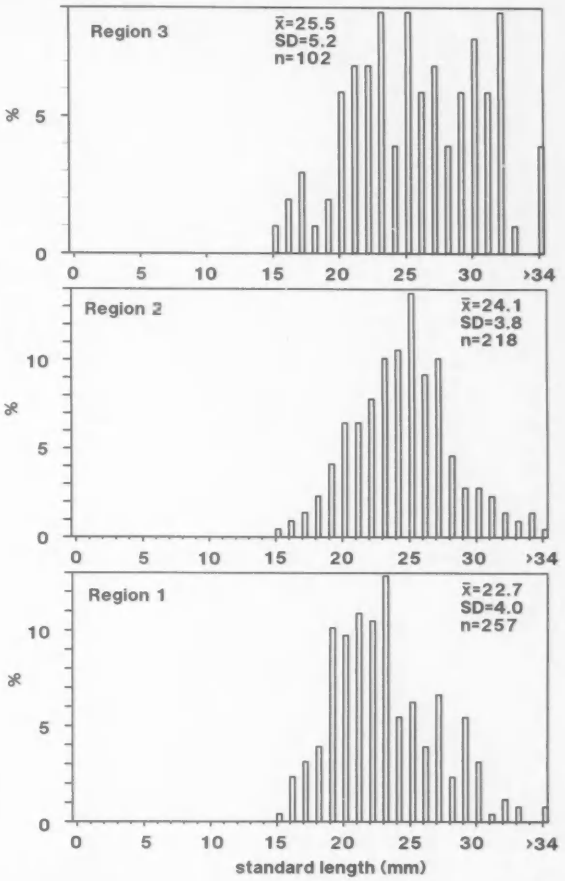

FIG. 9. Regional size frequency distributions of pelagic juvenile cod sampled during cruise 87-1 across the three regions. Probability values for K.S. comparisons for Tucker trawl: region 1,2; 0.01*, region 2,3; 0.17, region 3,1; 0.01. * refers to statistically significant differences.

frequency distributions of the larvae and juveniles across the three regions were significantly different in some cases, but in all but one comparison the size differences were less than 3 mm. Thus, Cushing's (1986) criticism of O'Boyle et al. (1984), that a spatial separation of eggs, larvae, and juveniles would have been observed had a larger net been used to sample the larger individuals, is probably not valid for southwestern Nova Scotia. It is evident that had there been a spatial gradient in size, the effect of sampling gear on our perception of the distribution would have been considerable.

The distribution of larval and pelagic juvenile cod, although similar to one another within years, varied dramatically between years. The percentage of larvae and juveniles in the offshore was the least in 1985 and greatest in 1987. This is corroborated by both positive and negative correlations of juvenile cod with distance from Browns Bank from 1985 to 1987 (Fig. 3). The inter-annual comparisons support our claim that meaningful conclusions about distributional patterns during the early life history cannot be made from single year surveys.

The range in size of cod larvae was similar between the three regions which could imply broad-scale, protracted spawning by cod. However, this interpretation was found wanting in light of the following evidence. Most cod that spawn during March and April in southwestern Nova Scotia do so on Browns Bank. Seasonal groundfish surveys conducted in NAFO Division 4X show that ripe female cod are concentrated on Browns Bank during March (Scott 1983). The results of past Scotian Shelf ichthyoplankton surveys have shown that peak concentrations of cod eggs were centred on Browns Bank during March and April (Gagne and O'Boyle 1984; O'Boyle et al. 1984). Five ichthyoplankton cruises, conducted independently of our study, from February to June 1985 in southwestern Nova Scotia showed cod egg abundance peaked in April with 95% of the eggs in region 1, with the majority occurring inside the 100-m isobath of Browns Bank (P.C. Hurley, Marine Fish Division, Bedford Institute of Oceanography, N.S. B2Y 4A2, pers. comm.). Coastal spring spawning may occur along the southern shore of Nova Scotia, but its magnitude relative to the offshore appears slight (Gagne and O'Boyle 1984).

The circulation features characteristic of Browns Bank may explain the variable inter-annual distributions of cod larvae and juveniles. A permanent clockwise gyre is situated over the western cap of Browns Bank, with an average residence time of 14 d (5–25 d range), episodically disrupted by winds persisting over a few days (Greenberg 1983; Smith 1983, 1989). North of Browns Bank a residual current flows westward and then northward towards the Bay of Fundy at 1–8 km·d^{-1} (seasonal average). Depending upon wind stress reversals in flow can

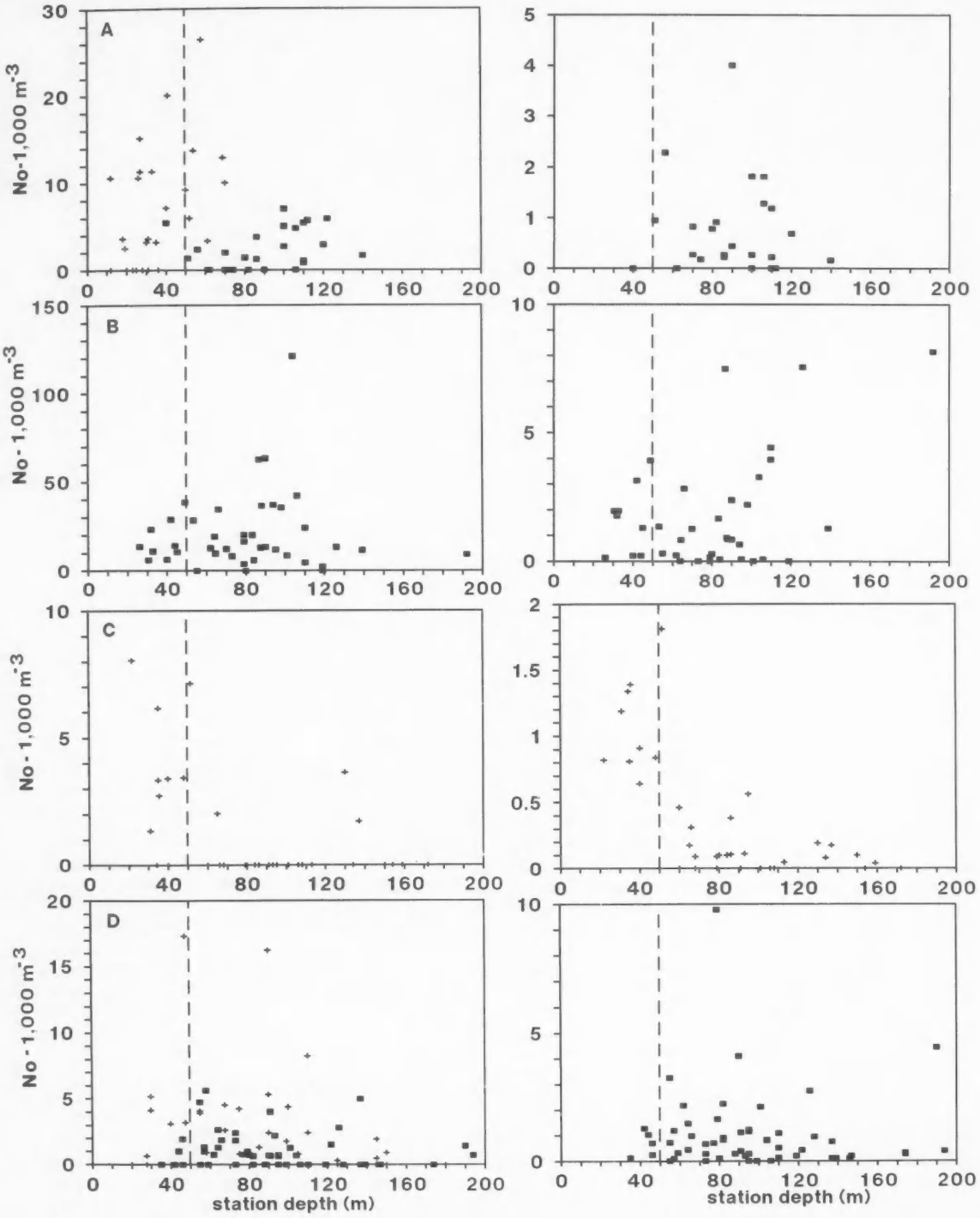

FIG. 10. Relationship between cod density and depth estimated by small (left-hand column) and large (right-hand column) gear types. Stations from Browns Bank were excluded. Broken line shows 50-m depth which is the limit of past offshore ichthyoplankton surveys conducted in southwestern Nova Scotia. Stations sampled on exploratory cruises are designated by +. (A) cruise 85-1 (B) cruise 86-1,2, (C) 5–12 June 1986, (D) cruise 87-1.

occur at daily intervals (Smith 1989). Smith (1989) concludes that 60–80% of the total variance in current variability is due to high frequency wind events in the 2–10 d band, a phenomenon confirmed by the variable drogue tracks.

The occurrence of young cod on Browns Bank, particularly in 1987 (Fig. 8), is consistent with the observation of O'Boyle et al. (1984) that the gyre acts to retain larvae. Obviously, this situation was not true in other years of our study (Fig. 4, 6). The location of juvenile cod should, in part, be determined by the magnitude of displacement of eggs and larvae from the spawning site. In our study pelagic juveniles were, on average, 30 d older than the larvae during 1985 and 1986 (I. M. Suthers, unpubl. data), yet the spatial distributions did not reflect the additional period of drift. This supports the notion of pelagic juveniles limiting further horizontal displacement (e.g. through behavioural means), and is one explanation for the mixture of sizes observed during all of the surveys. We use the term "retention" to describe the apparent persistence of young cod in time and space; whether the fraction of pelagic juveniles remaining near Browns Bank are members or vagrants of that population (Sinclair 1988) remains to be determined.

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An Age- and Temperature-Mediated Growth Model for Cod (*Gadus morhua*) and Haddock (*Melanogrammus aeglefinus*) Larvae in the Gulf of Maine[1]

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Campana, S. E., and P. C. F. Hurley. 1989. An age- and temperature-mediated growth model for cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) larvae in the Gulf of Maine. Can. J. Fish. Aquat. Sci. 46: 603–613.

While field studies of larval fish growth require an easily parameterized growth model, simple relationships between size and age are seldom applicable to other populations and/or environments. The model presented here attempts to bridge the gap between simple age–length regressions and more sophisticated experiment-based models by incorporating a temperature term as a function of absolute growth rate. Growth is assumed to be logistic, with temperature influencing growth rate parabolically on a daily basis. The integrated form of the model provides an estimate of length-at-age of the larva. When fitted to a variety of independent cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) data sets collected in the Gulf of Maine, the model performed with minimal bias despite the absence of a food availability term. Larval age data were generated through validated otolith microstructure examinations, although the resolution limits of light microscopy introduced a small degree of bias (2–3 d) into the estimates. The daily temperature record was generated from a sinusoidal model using monthly mean temperatures. Since otolith microstructure examination and remote sensing of temperature are established techniques, this model may prove useful in other larval studies.

Bien que les études de croissance des larves de poisson réalisées sur le terrain doivent pouvoir se fonder sur un modèle de croissance facilement paramétrisé, il est rarement possible d'appliquer des rapports simples entre la taille et l'âge à d'autres populations et/ou d'autres milieux. Le modèle présenté ici tente de combler le vide entre les régressions simples âge-longueur et les modèles plus sophistiqués, élaborés à partir d'expériences, en incorporant un terme de température, qui est fonction de la vitesse de croissance absolue. La température joue un rôle sur la vitesse de croissance de façon parabolique sur une base quotidienne. La forme intégrée du modèle fournit une estimation de la longueur en fonction d'un âge donné de la larve. Le modèle, appliqué à diverses séries de données indépendantes sur la morue (*Gadus morhua*) et l'aiglefin (*Melangrammus aeglefinus*) prélevés dans le golfe du Maine, a présenté un biais minimum malgré l'absence d'un terme de disponibilité de nourriture. Les données sur l'âge des larves ont été produites par des examens validés des microstructures des otolithes, bien que les limites de résolution de la microscopie optique aient introduit un petit biais (2–3 d) dans les estimations. Une liste des températures journalières a été produite à partir d'un modèle sinusoïdal fondé sur les températures moyennes mensuelles. Étant donné que l'examen des microstructures d'otolithes et la télédétection des températures sont des techniques reconnues, ce modèle pourrait servir à d'autres études sur les larves.

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Predictive growth models for larval gadids span the range from simple linear regression of length on age (Anderson 1982; Yin and Blaxter 1986) to sophisticated environment-mediated foraging calculations (Beyer and Laurence 1981; Ellertsen et al. 1981). The degree of sophistication and predictive power in these studies is often inversely related to the level of the experimenter's control; complex models are not easily parameterized in field situations, nor are they necessarily intended to be. Yet realistic growth models of wild fish larvae often form the basis for models of higher-order processes such as recruitment and survival (e.g. Jones 1973; Leak and Houde 1987). The realities of monitoring the growth and environment of marine larvae in situ have constrained previous workers to the fitting of imprecise and/or point specific length-at-age curves. For this reason, we see the need for an easily-parameterized growth model of intermediate complexity, with powers of prediction for wild larvae, and the flexibility necessary for application to a broad range of environmental conditions and/or populations. Such a model is presented here in application to larval cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) in the Gulf of Maine.

Current models of the growth of larval cod and haddock are largely based upon the results of laboratory (Laurence 1974, 1978; Beyer and Laurence 1981; Laurence et al. 1981; Gamble and Houde 1984; Yin and Blaxter 1986) and enclosure (Ellertsen et al. 1981; Gamble and Houde 1984; Kvenseth 1984) studies. Growth data were modelled primarily as a function of age, with prey availability, temperature, and other variables incor-

[1]Fisheries Ecology Program Contribution Number: 5.

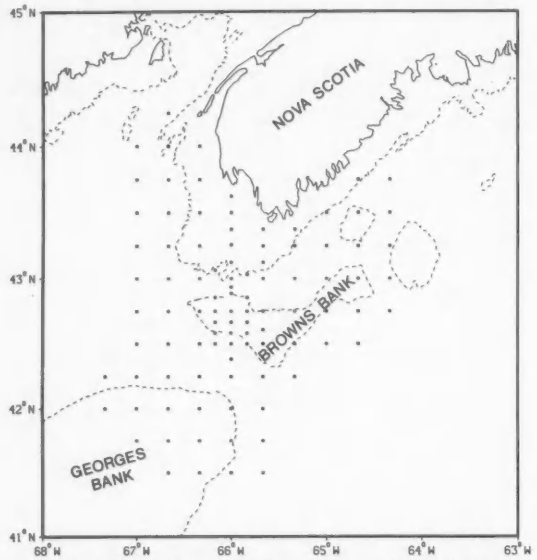

FIG. 1. The location of sampling stations relevant to this study during the ichthyoplankton survey of southwest Nova Scotia in 1984 and 1985. Coverage of the survey grid varied slightly among cruises (Table 1).

TABLE 1. Summary of cruises represented in this study.

Year	Cruise	Date	Number of stations sampled	Number of larvae examined	
				Cod	Haddock
1984	H114	March 12–30	54	7	67
	H116	April 16–27	59	100	—
1985	H130	Feb. 4–22	93	15	—
	H132	March 11–29	49	42	7
	H133	April 2–17	90	202	40
	H135	May 6–16	57	95	136
	H137	June 3–14	59	35	372

porated as accessory variables into the more complex models. While age data are intrinsic to controlled experiments, they have (until recently) been difficult to obtain in field studies. Therefore, earlier field studies of larval cod and haddock growth necessarily adopted length-frequency analysis as a proxy for age, despite the confounding effects of immigration/emigration, size-selective mortality and an extended spawning period (Graham 1933; Saville 1956; Anderson 1982). All of these effects can skew a length-frequency mode, thus making it difficult or impossible to track a larval cohort and/or assess its rate of growth. With the advent of otolith microstructure examination as a more precise age determination tool (Pannella 1971; Brothers et al. 1976; reviewed by Campana and Neilson 1985), direct age measurements of field-collected larvae became possible. Such measurements have been used to advantage in other field studies of larval gadoids (Nishimura and Yamada 1984; Walline 1985; Kendall et al. 1987), as well as in the only other field study of larval gadid age structure in the Gulf of Maine (Bolz and Lough 1983). It is also the approach adopted here.

In this paper, we wish to reassess the results of Bolz and Lough (1983) in light of recent findings concerning apparent bias in otolith microstructure studies (Geffen 1982; Campana et al. 1987), as well as extend the scope of their study beyond that of a point estimate. Accordingly, we shall evaluate the spatio-temporal variation in larval growth rate over a broad region and sequence of surveys, encompassing the waters in and around Browns and Georges Bank in 1984 and 1985. A third objective is to develop a generalized growth model to fit these data, with the view towards making it broadly applicable to other areas and times. Finally, we use the model to test competing hypotheses concerning the relative growth of cod and haddock larvae under a variety of environmental regimes (Laurence 1978; Laurence et al. 1981).

Materials and Methods

Cod and haddock larvae were collected in seven different cruises over a fixed survey grid as part of the Fisheries Ecology Program ichthyoplankton survey. The survey encompassed 97 stations to the south, east, and west of Nova Scotia, down to and including portions of Georges Bank (Fig. 1). Surveys represented in this study were conducted in March and April of 1984 and monthly between January and June of 1985, although weather restricted grid coverage on some cruises (Table 1). Each station was sampled with paired bongo nets fitted with 61-cm frames, 333-μm Nitex mesh, and mouth-mounted flowmeters. Tows were made obliquely to within 5 m of the bottom (to a maximum of 200 m) and immediately replicated. Full sampling details and cruise-by-cruise station locations are documented elsewhere (P.C. Hurley and S.E. Campana, unpubl. data).

Upon collection, unsorted samples were preserved in 5% formalin: saltwater made basic to a pH of 8.0–9.0 with sodium carbonate; the latter retarded acidic degradation of the otoliths until the samples could be preserved in 95% ethanol. Samples were transferred to 95% ethanol for storage within 3 wk of collection. Prior to otolith removal, larvae were measured to the nearest 0.1 mm. Both pairs of sagittal and lapillar otoliths were removed, cleansed of adhering tissue, and mounted individually on microscope slides with Krazy Glue according to standard techniques (Campana and Neilson 1985). All otoliths with diameters exceeding 40 μm were polished with lapping film prior to microscopic examination. Otoliths showing evidence of formalin degradation (brown discolouration, pitting) were not considered further. Degraded otoliths constituted approximately 20% of the total number (primarily in Cruise H135), although the proportion degraded within a sample varied substantially among samples. Microstructural examinations were made with a research quality compound microscope at 1250×; the functional resolution limit of this system was previously estimated to be 0.25 μm (Campana et al. 1987). Measurements of otolith and hatch check diameter were made with an ocular micrometer to the nearest micrometre, with the difference between the two measurements hereafter defined as the growth diameter. Criteria for definition of the hatch check were those of Bolz and Lough (1983); Bergstad (1984); and Dale (1984). All daily increment counts were replicated by the same reader. Unless stated otherwise, the mean measurement and count values for each otolith type within a larva were used in all analyses.

Indices of potential resolution loss during increment counts were generated through the increment width estimation procedure described in Campana et al. (1987). Briefly, this involved the fitting of a logistic curve to the increment count data associated with each otolith growth diameter (OGD = otolith diameter — hatch check diameter), and then using the fitted model

TABLE 2. Sinusoidal model used to generate a daily sea surface temperature record from mean monthly temperatures. Separate models were developed for Browns and Georges banks in each of 1984 and 1985. DOY = day of year.

$$\text{Model: Temp(°C)} = \left(a\text{Sin}\left(\left(\frac{2\pi}{365}(\text{DOY} + b)\right)\right)\right) + c$$

		Parameter estimate				Estimated temperature		
Region	Year	a	b	c	R^2	Jan. 1	March 1	June 1
Browns	1984	5.350	−158.5	8.417	0.98	6.2	3.1	7.7
	1985	5.301	−161.1	8.355	0.99	6.4	3.1	7.4
Georges	1984	5.088	−156.9	9.616	0.99	7.4	4.6	9.1
	1985	5.187	−159.5	9.290	0.97	7.2	4.2	8.5

TABLE 3. Increment width at Age 1 day in the otoliths of cod and haddock larvae collected on several cruises. The 1984 larvae were collected on Georges Bank while the 1985 samples were from the vicinity of Browns Bank. Widths were estimated for each otolith type from the logistic model relating increment count to otolith growth diameter in each larva (see text for details). * = Poor fit of model (pattern in residuals), rendering width estimation inappropriate.

	Increment width (μm) at Age 1 day			
	Cod		Haddock	
Cruise date	Lapillus	Sagitta	Lapillus	Sagitta
1984; March 12–30	0.33	0.40	0.54	0.33
1985; March 11–29	0.42	0.42	—	*
April 2–17	0.37	0.43	0.45	*
May 6–16	0.39	0.37	0.44	*
June 3–14	0.25	0.19	0.53	0.63

to estimate increment width in the first few days posthatch. Specifically, OGD was related to increment count (C) in the logistic equation

$$\text{OGD} = a + b(1+\exp(-c(C-d)))^{-1},$$

where a, b, c, and d are model parameters. Increment width on Day i was then calculated as $(\text{OGD}_i - \text{OGD}_{i-1}) \div 2$ for each of the samples.

To determine the frequency of increment formation in newly-hatched cod larvae, samples of known age larvae were obtained incidentally from two separate experiments conducted by J. D. Neilson and K. G. Waiwood of the St. Andrews Biological Station, N.B. In both experiments, larvae were reared from the egg stage under a diel light cycle (12 h light:12 h dark) and ambient temperatures of 5–6°C (Exp. 1: 29 April–13 May 1983, N = 42; Exp. 2: February 7–March 4, 1984, N = 8). Larvae were fed twice daily with rotifers. Sampled larvae were preserved in 95% ethanol prior to otolith removal. Microstructural examinations were made as described above without knowledge of true larval age or sampling frequency.

Vertical temperature profiles were made at each cruise station. However, retrospective analysis of larval growth required a daily sequence of water temperatures. Daily temperature series for 1984 and 1985 were generated from mean monthly temperatures (NOAA 1984, 1985) in two areas: Browns and Georges banks. Sinusoidal least-squares regressions were fit to the monthly data, with the resulting equations used to predict the daily sea surface temperature (SST) record for each region (Table 2). The predicted temperature values were consistent with those actually observed during each cruise.

TABLE 4. Results of the first experiment reporting the frequency of increment formation in newly hatched cod larvae.

Experiment 1.

Model: Increment count = $a + b$ (Age)
Range of ages = 0–14
N = 42
$P < 0.001$
R^2 = 0.80

Parameters:	Estimate	SE	Significance
Intercept	−0.45	0.63	0.48
Slope	0.89	0.069	<0.001

TABLE 5. Results of the second experiment reporting the frequency of increment formation in newly hatched cod larvae.

Sample	N	Age (d)	Mean count
1	3	14	17
2	2	16	15
3	2	4	7
4	1	26	16

Parameters for larval and otolith growth models were generated for two regions: Browns Bank/Southwest Nova Scotia, and Georges Bank; based upon presumed stock boundaries (Bowen 1987) and hydrographic regimes (Smith 1983; Perry and Hurley 1986). All linear and nonlinear regression parameters were estimated by least squares methods. Residuals from the models were given careful examination, particularly near the origin. Models were accepted only in the absence of patterns in the residuals. The significance level was set at 0.05 for all tests.

Results and Discussion

Estimation of Age, Resolution Loss, and Length

The otolith microstructure of the cod and haddock larvae was largely unambiguous in its interpretation. Intra-larval increment counts were highly correlated both within an otolith type and between lapillae and sagittae (slope = 1.0 ± 0.05; $R^2 > 0.95$) in both species. However, the intercept term for the regression of sagittal counts on lapillar counts was highly significant, and indicated that the latter exceeded the former by an average of 2.6 and 1.6 for cod and haddock, respectively. Given the smaller size of the sagittae at hatch and the very narrow (<0.5 μm) increments encircling the nucleus (Bolz and Lough 1983; 1989), Campana resolution limitations associated with the use of light microscopy were suspected to be the source of the inter-otolith discrepancy (Campana et al. 1987). The significance of this

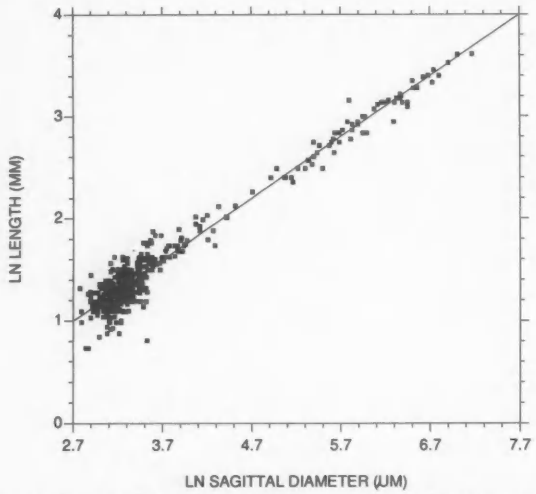

FIG. 2. Regression of cod larval length on maximum sagittal diameter, with both axes ln transformed. Since the unaggregated relationships were not significantly different among themselves, cod data were aggregated across years, cruises, and regions.

suspicion is that increment counts would underestimate the number actually present if increments were too narrow to resolve as individual units. In the case of larval herring (*Clupea harengus*), resolution-limited increment counts resulted in serious underestimates of age (15–20 d) (Campana et al. 1987). The existence of a significant, within-larva correlation ($P < 0.01$) between the intersagittal differences in growth radius and increment count, confirmed the presence of resolution-limited increment visibility in all large samples of cod and haddock larvae. Since a significant relationship was also observed among the lapilli, estimates of the magnitude of the resolution loss were deemed necessary.

Increment widths at age from each of the cruise collections were compared both with the functional resolution limit of our microscope system, and among themselves, in order to assess the relative magnitude of the potential count bias. Increment widths at day 1 were close to the resolution limit of our system for sagittae and lapilli in both cod and haddock in all cruises (Table 3). However, the increment widths increased rapidly with age, suggesting that unresolved increments, if they existed, were associated only with the youngest larvae. Haddock increment widths at day 1 tended to be larger than those of cod.

The validity of using increment counts to estimate the age of cod and haddock larvae was assessed in the first validation experiment. Increment counts were highly correlated with age in both sagittae and lapilli (Table 4). In addition, a daily frequency of increment formation in the lapilli was indicated by a regression of increment count on age not significantly different from 1.0. However, the regression slope was significantly less than 1.0 for the sagittae, and indeed, increment counts tended to underestimate age in both otolith types. Since the age-increment discrepancy stabilized in both otolith types before day 10 (asymptotic discrepancy = 2–3 and 5–6 for lapilli and sagittae, respectively), resolution limitations induced by light microscopy were again suspected. The generally good fit between the ages and increment counts in Exp. 2 (Table 5) was also consistent with resolution-limited visibility, since the one poorly-predicted age was associated with a very slow-growing larva.

In a procedure analogous to that applied to the wild larvae, increment width at day 1 was estimated for the known age larvae in Exp. 1. The resultant values (lapilli, 0.31 µm; sagittae, 0.36 µm) fell within the lower range observed among the wild larvae (Table 3), and were probably not different from our functional resolution limit. Accordingly, we have assumed that increment counts in the wild larvae underestimated larval age to an extent similar to that observed in the laboratory. Given hatch check formation in larval cod on day 1 (Bergstad 1984; Dale 1984), and the close similarity of haddock otolith microstructure to that of cod (Bolz and Lough 1983; Campana 1989), our daily increment counts appear to have underestimated age in these two species by 1–2 and 4–5 d for the lapilli and sagittae, respectively; this level of bias was considered both acceptable and unavoidable. Therefore, estimates of larval age were calculated by adding one (corresponding to the age at hatch check formation) to the mean count in the lapilli (or sagittae, if larger).

Variability is introduced into measurements of larval length through factors such as net handling time, preservation schedule, etc. (Radtke and Waiwood 1980; Fowler and Smith 1983), all of which may deform the soft tissues of a larva and vary in magnitude from sample to sample. This variability was reduced through use of sagitta length as a correlate of total length in cod larvae. The rigid sagittae can be precisely measured, are unaffected by factors other than those that cause dissolution, and were linearly related to larval length after ln-ln transformation (Fig. 2), as in

$$\ln L = 0.5996 \cdot \ln Sag - 0.6199 \quad N = 507; R^2 = 0.95,$$

where L = total length of the larvae (millimetres) and Sag = maximum sagittal length (micrometres). Tests for a variety of factor effects indicated that the assumption of a common slope and intercept was justified across regions, cruises and years (ANCOVA, $P > 0.1$) (S. E. Campana 1989). Accordingly, sagittal measurements were used to more precisely estimate cod larval length in the growth models that follow. While at first glance similar relationships could have been generated for haddock larvae, and for lapilli of both species, consistent (albeit minor) patterns in the residuals among cruises suggested that they not be applied (Campana 1989).

Growth as a Function of Age

On a cruise-by-cruise basis, cod (Fig. 3) and haddock (Fig. 4) larval length was successfully modelled as a function of age, using the exponential equation

$$L = \exp(a + b \cdot \text{age}),$$

where a and b are regression parameters. All model fits were unbiased and highly correlated, with the correlation coefficients for cod generally exceeding those for haddock (Table 6). While specific growth rates for cod and haddock did not differ significantly within a cruise and region, such an analysis is of little value without reference to the range of ages present in the data; this fact is also at least partially responsible for the differing magnitudes of the correlation coefficients between species.

Attempts to fit the exponential model of larval growth to data aggregated on a regional (Browns versus Georges banks) and/or yearly basis were unsuccessful; the residuals formed a clear pattern across ages and cruises. While use of the log-transformed logistic model

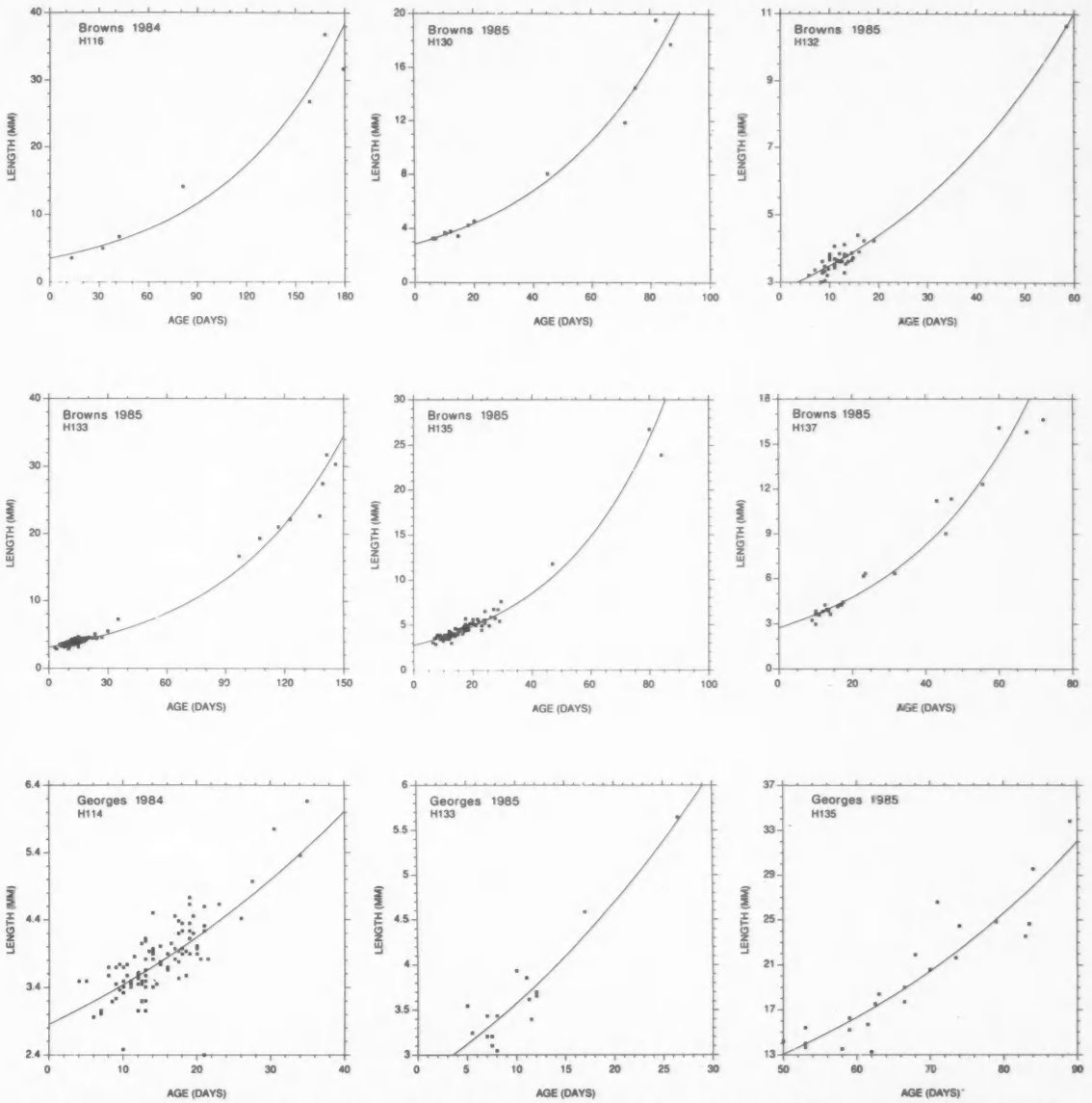

FIG. 3. Exponential growth models for cod larvae collected on each of seven cruises on Browns and Georges banks in 1984 and 1985.

$$\text{Ln}\, L = \text{Ln}\,(a + b \div (1 + \exp(-c(\text{age} - d)))),$$

where a, b, c, and d are model parameters, improved the overall model fit, strong trends in the residuals persisted when examined on a cruise-by-cruise basis.

Development of an Age- and Temperature-Mediated Growth Model

Given the inadequacy of the simple age-based models in application to the aggregated regional data sets, more complex models were developed which incorporated temperature as an accessory variable. Temperature is widely recognized as a significant modifier of the growth rate of fishes. Justification for the inclusion of temperature in this study was based upon laboratory demonstrations of temperature-mediated growth rates in gadid larvae (Laurence 1978; Buckley 1984). Further justification was derived from this study in the form of a significant relationship between mean SST during each cruise and the calculated specific growth rate of cod larvae less than 30-d old in each cruise collection ($P = 0.02$, $R^2 = 0.64$). While the relationship was not significant for haddock larvae, the haddock data exhibited a similar trend. Established principles concerning temperature effects on growth processes (Brett 1979; Ricker 1979) suggested the need for a logistic growth model where temperature influenced absolute growth rate in a parabolic fashion. However, in keeping with the principle of parsimony, model development began with the simplest possible formulation, progressing to more complex designs only if the statistical criteria for the simpler model were not met.

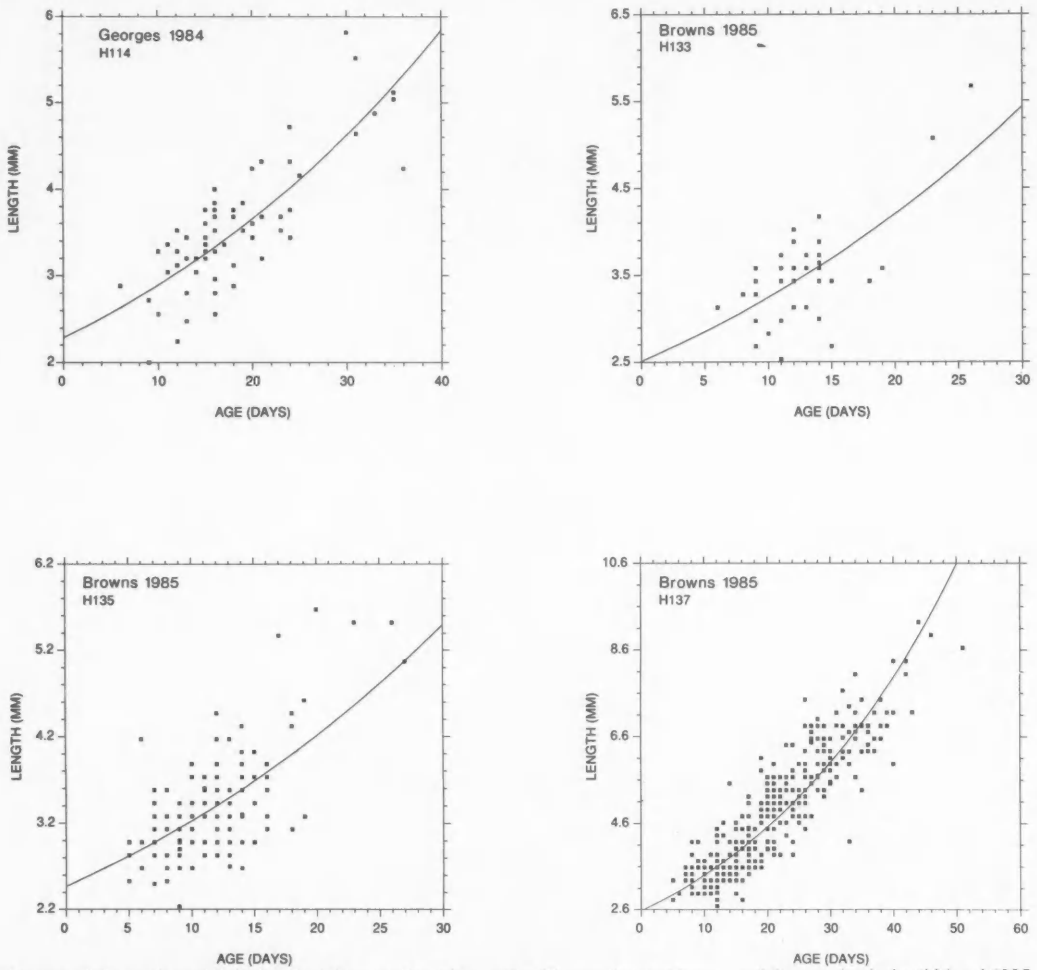

FIG. 4. Exponential growth models for haddock larvae collected on each of four cruises on Browns and Georges banks in 1984 and 1985. Model statistics are presented in Table 6.

TABLE 6. Parameters and diagnostics of an exponential growth model $L = \exp(a + b \cdot \text{age})$ fitted to cod and haddock larvae (Fig. 3 and 4) on a cruise-by-cruise and regional basis. All models were highly significant. Specific growth rates (percent·d^{-1}) for each cruise, region, and species are also presented.

				Intercept (a)		Slope (b)				
Species	Region	Year	Cruise date	Estimate	SE	Estimate	SE	N	R^2	Specific growth rate
Cod	Browns	1984	April 16–17	1.24	0.13	0.0133	0.0011	7	0.97	1.33
		1985	Feb. 4–22	1.04	0.03	0.0217	0.0001	14	0.99	2.18
			March 11–29	1.02	0.02	0.0230	0.0012	39	0.91	2.30
			April 2–17	1.13	0.01	0.0161	0.0002	184	0.97	1.61
			May 6–16	1.02	0.02	0.0278	0.0009	69	0.94	2.78
			June 3–14	1.01	0.04	0.0275	0.0011	24	0.96	2.75
	Georges	1984	March 12–30	1.04	0.03	0.0186	0.0018	100	0.52	1.86
		1985	April 2–17	1.00	0.04	0.0272	0.0033	16	0.83	2.72
			May 6–16	1.45	0.14	0.0225	0.0020	24	0.85	2.25
Haddock	Browns	1984	March 12–30	0.828	0.044	0.0234	0.0023	67	0.61	2.34
		1985	April 2–17	0.920	0.070	0.0258	0.0053	38	0.40	2.58
			May 6–16	0.905	0.034	0.0266	0.0028	130	0.41	2.66
			June 3–14	0.941	0.017	0.0284	0.0007	370	0.79	2.84

The heterogeneity of larval ages evident in all of the samples implies that the history of temperature exposure will have differed for most larvae. Because the growth response to temperature is seldom constant across all ages/sizes (Ricker 1979), any calculations for a daily growth–temperature interaction would have to be estimated for each individual larva. The simplest form of such an interaction is that of a linear relationship between absolute growth rate and temperature, or equivalently, the hyperbolic or degree–day relationship of salmonid egg development models (Ricker 1979). This form of interaction assumes a growth response to temperature analogous to that of metabolic rate, but is formulated to deal with the changes in absolute growth rate that often occur as a fish ages. Because it is virtually impossible to monitor the growth rate of individual wild fish on a daily basis, the model was integrated to reflect larval length-at-age upon sampling, as in

$$(1)\quad L_{age} = L_{hatch} + \int_{t=0}^{age} (\text{Absolute growth rate} \times \text{Temperature})\, dt$$

The form of the absolute growth rate term ($^{dL}/_{dt}$) depends on the model selected, but since the exponential model described earlier was applied successfully on a cruise-by-cruise basis, it was also the initial choice here. This results in:

$$(2)\quad L_{age} = L_{hatch} + \int_{t=0}^{age} (aGe^{Gt} \cdot T_t)\, dt$$

and the discrete approximation:

$$(3)\quad L_{age} = L_{hatch} + \sum_{t=0}^{age} (aGe^{Gt} \cdot T_t),$$

where L_{hatch}, a, and G are model parameters, G is the instantaneous (or specific) growth rate, T_t is temperature on the appropriate Julian day, and t is time (days). The term aGe^{Gt} is the derivative of the exponential growth model, or equivalently, the absolute growth rate at age t. Using the daily temperature record (Table 2) and the age of each larva, model (3) was fit to the data from Browns Bank in 1985. The Browns Bank data were selected since they represented the largest regional data set ($N = 507$ for cod; $N = 545$ for haddock) and the broadest temperature range through the time series: 3–11°C.

The fit of the model initially appeared to be quite good ($R^2 = 0.93$ and 0.81 for cod and haddock, respectively), but examination of the residuals as a function of age indicated that the model seriously overestimated the length of larvae older than 90 d. Accordingly, the model was altered to reflect a more realistic growth form, the logistic equation, in conjunction with a linear temperature interaction. The fit of this model was better than that of model (3), but persistant patterns in the residuals were identified among the older larvae of the February cruise (H130) and the younger larvae of the June cruise (H137). Since these two sets of larvae would have experienced the highest temperatures of the sampling season (>10°C), it is likely that such temperatures would have exceeded the larval growth optimum. Temperature optima are well documented in temperate fishes (see review by Brett (1979)) and would be expected in cod and haddock stocks nearing the southern limit of their range. Growth–temperature optima were modelled in this study through use of a quadratic parabola, which has been used successfully in many other studies of fish growth (Ricker 1979). The parabolic temperature term was initially incorporated into a modification of model (3); allying exponential growth (the most parsimonious model) with an inverse parabolic temperature term, the latter served to increase absolute growth rate parabolically to a temperature-based optimum, after which growth rate decreased.

The fit of this model was again good for both species, but it produced trends in the residuals for the oldest larvae. These results suggested that the temperature parabola was effective, but that exponential growth could not be assumed in older fish. Accordingly, the latter two models were merged to incorporate both logistic growth and a parabolic temperature interaction, resulting in

$$L_{age} = L_{hatch} + K \int_{t=0}^{age} \frac{\text{d(logistic)}}{dt} \cdot (c - (T_t - T_{opt})^2)\, dt$$

and the numerical approximation:

$$(4)\quad L_{age} = L_{hatch} + K \sum_{t=0}^{age} (Gl_t - Gl_t^2 L_\infty^{-1})\,(c - (T_t - T_{opt})^2),$$

where $l_t = L_\infty(1 + \exp(-G(t-t_0)))^{-1}$; G, L_∞, t_0, c, and T_{opt} (= temperature optimum) are model parameters; and L_{hatch} and K are fixed at 3.0 and 0.2, respectively. While the fixed value of L_{hatch} was somewhat arbitrary, model results were insensitive to the specific value within the range of 2–5 mm. The fit of this model to the aggregated Browns Bank data was excellent ($R^2 = 0.96$ and 0.83 for cod and haddock, respectively) and appeared to be unbiased across all combinations of cruise, length, and age (Fig. 5; Table 7). The fit was particularly good for the cod larvae, and given the range of months, temperatures, ages, and lengths present in the data, it would appear to be a robust predictor of larval length. Use of five different cruise collections in the test data set precluded any collinearity between temperature and age. Of course, the predictive power of any model decreases near the extremes of the data range, and this effect is to be particularly expected for the largest cod larvae; the potential for avoidance of the bongo gear is almost certainly present in larvae >10 mm (I. Suthers, Department of Biology, Dalhousie University, Halifax, N.S., pers. comm.) and would be expected to result in preferential capture of the slower growing individuals. It is unlikely that gear avoidance had a significant effect upon the size-at-age estimates of the much smaller haddock larvae. However, the restricted ranges of the haddock age, length, and temperature data constrained the utility of the growth model to larvae less than 35–40 d old.

The predictive capability of the model was assessed through tests with independent data sets. Growth projections for cod and haddock on Browns and Georges banks in 1984, and on Georges Bank in 1985, were made using the parameters in Table 7, resulting in predictions similar to those actually observed; in all cases, the mean residual was approximately 0. Slight trends were observed in the residual patterns of cod from cruises H116 (1984; Browns) and H135 (1985; Georges), and in haddock from H114 (1984; Georges), but the source of the discrepancy was difficult to pinpoint. There is no question that imprecision in the estimated temperature record could have resulted in the predicted growth anomalies; simulations with the temperature data verified this. An equally viable explanation is the absence of food availability/consumption as a term in the growth model. Since food consumption is known to influ-

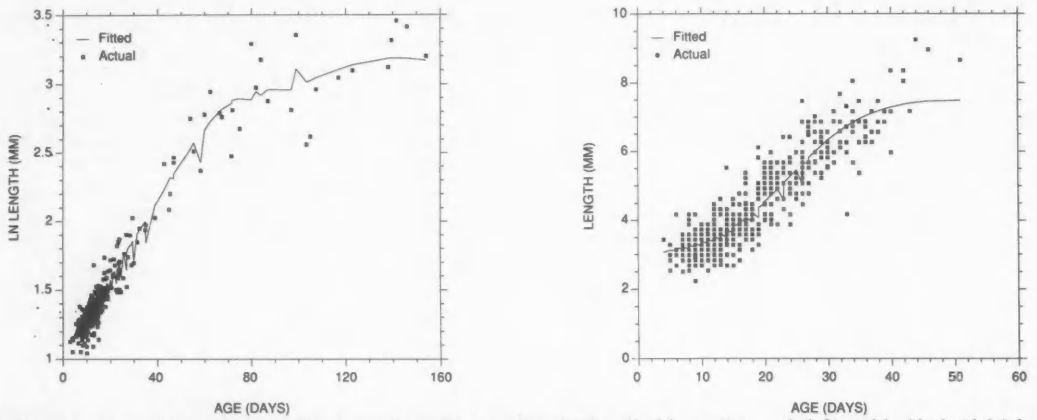

FIG. 5. Fit of an age- and temperature-mediated growth model (equation (4), described in text)) to cod (left) and haddock (right) larvae on Browns Bank in 1985. Data were aggregated across cruises. The model assumes logistic growth and a parabolic relationship between temperature and absolute growth rate on a daily basis. The fitted line appears irregular since only one of the two independent variables is plotted. Model results are summarized in Table 7.

TABLE 7. Parameter estimates, associated error terms, and ANOVAs for a model integrating logistic growth and a parabolic temperature term in the estimation of larval length (see model (4) in text). The model was fit to both cod (ln-transformed) and haddock (untransformed) data collected on and around Browns Bank in 1985.

Species	Source of error	Sum of squares	*df*	Mean square	R^2	Parameter	Coefficient	SE
Cod	Model	875.81	5	175.16	0.96	G	0.05016	0.00274
	Error	3.2169	357	0.00901		L_∞	59.18	13.44
						t_0	60.57	2.33
						c	22.77	4.44
						T_{opt}	5.925	0.195
Haddock	Model	11047	5	2209.5	0.83	G	0.1571	0.0110
	Error	158.02	539	0.29318		L_∞	5.467	5.081
						t_0	24.44	0.89
						c	44.00	39.79
						T_{opt}	6.701	0.936

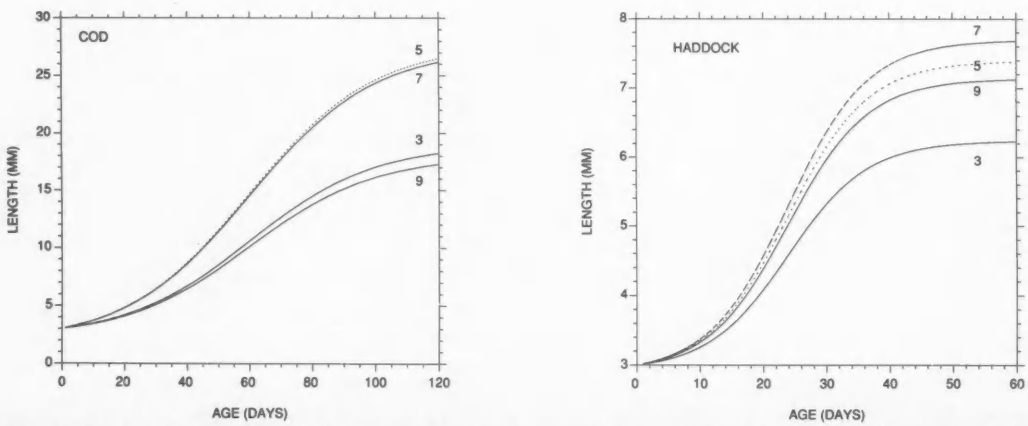

FIG. 6. Growth projections for cod and haddock larvae at various constant temperatures as predicted from model 4 (described in text). Digits refer to the temperature in degrees Celsius.

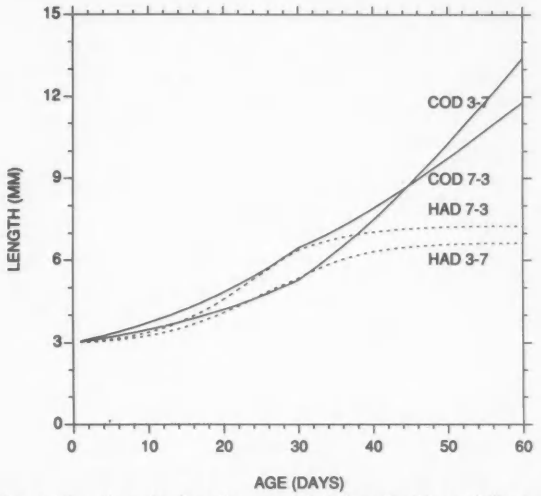

FIG. 7. Growth projections from model 4 (described in text) for cod and haddock larvae under interrupted temperature regimes. Temperature was held constant at one temperature (3° or 7°C (first digit in label)) for 30 d, following which it was shifted to a second temperature (3° or 7°C (second digit in label)) for the remaining 30 d. Temperature had the most sustained effect on growth when absolute growth rate was greatest.

ence the growth of larval cod and haddock (Laurence 1974; Laurence et al. 1981; Ellertsen et al. 1981), food availability may differ enough spatially and temporally to introduce error into the model projections. It is important to note however, that the model residuals from five independent data sets were invariably small, and equally explicable in terms of prey concentration or temperature anomalies. Given the level of precision required here, and the close correspondence between temperature and prey abundance in many ecosystems, the distinction between these latter two factors may be irrelevant in the context of this model.

Comparative Growth of Cod and Haddock Larvae

The logistic form of the growth equation used here has been fitted to length-at-age data from a wide variety of other species (Bailey 1982; Nishimura and Yamada 1984; Boehlert and Yoklavich 1985; Crecco and Savoy 1985; Warlen and Chester 1985). With the incorporation of the temperature term as a function of absolute growth rate, temperature becomes a significant modifier of growth rate. Growth was optimized at a specific temperature in both species, in keeping with the parabolic form of the temperature terms (Fig. 6). The greater optimal temperature (T_{opt}) for haddock (6.7°C) over that of cod (5.9°C) is consistent with the distribution of each species along the eastern coast of North America.

Temperature exerted its most significant effect upon growth at the inflection point of the growth curve, where the rate of growth was most rapid. In the case of haddock, this occurred at an age of 20–30 d; the inflection point for cod was somewhat later (40–50 d). The influence of an age-structured temperature–growth rate relationship was demonstrated in growth projections where temperature was held constant at 3°C until age 30 d, after which it was shifted to 7°C until age 60 d; the converse temperature shift did not result in a comparable length at age 60 d, despite the equivalent number of degree–days in each 30-d interval, because of the higher size-structured growth rates in the older larvae (Fig. 7).

A comparison of the growth projections for each species indicates that neither has a substantial growth advantage within the temperature range of 3–7°C, at least until the age of 30 d (Fig. 6). After that age, haddock growth rate was reduced relative to that of cod, resulting in significant differences in size at age 50 at all temperatures. The inter-specific comparability of the growth curves noted here for young larvae is similar to that reported on Georges Bank (Bolz and Lough 1983; Buckley and Lough 1987) and in the laboratory (Laurence 1978). However, the divergence of the growth curves after approximately age 30 d is inconsistent both with Bolz and Lough's (1983) field study and with Laurence's (1978) laboratory work. Interestingly, a later study by Laurence (1981), in which cod and haddock larvae were forced to compete for food resources, produced an inter-specific growth divergence nearly identical to that reported here. Laurence (1981) discussed possible mechanisms for the divergence, including cannibalism, predation on haddock by cod, and prey size selectivity. Neither of our studies were designed to test among these hypotheses, but the similarity in results between his laboratory experiment and our field study is striking.

Predicted length-at-age values from our model are 30–40% less than those reported for Georges Bank by Bolz and Lough (1983). While the latter did not test for potential resolution losses in their interpretation of the otolith microstructure, our results indicate that these losses would have introduced little error into either of our estimates of age. The remaining procedural difference between the two studies was that associated with the measurement of larval length: Bolz and Lough (1983) applied Theilacker's (1980) shrinkage correction equation to all of their length data, while we did not. On the assumption that the observed cod lapillus diameter: larval length relationship was similar in both studies (Campana 1989), and given the resistance of lapilli to deformation/shrinkage, the observed lapillus diameters were used to calculate a common frame of reference for length between the studies. When Theilacker's (1980) equation was then applied to the standardized data, our prediction of cod larval length at the temperatures reported by Bolz and Lough (1983) fall within 3% of their estimates. While the consistency between the two independent growth estimates is remarkable, the question remains of whether or not to calculate growth on the basis of preserved or adjusted lengths. An unbiased estimate of live length would certainly be preferable. However, Theilacker's (1980) equation was designed for use with anchovy (*Engraulis mordax*) larvae, whose shape differs substantially from that of cod and haddock. It also results in cod shrinkage estimates on the order of 30%, which appears to be unreasonably high compared to the ~10% reported for silver hake (*Merluccius bilinearis*) larvae (Fowler and Smith 1983). Given the morphological similarity between larval silver hake and cod/haddock, we feel that a shrinkage estimate of ~10% is more representative of gadids. However, in the absence of a valid predictive equation for shrinkage, we have left our growth predictions uncorrected, in the knowledge that adjustments can always be made after the appropriate calibrations have been conducted.

Aside from the study of Bolz and Lough (1983), there are few studies with which to test the generality of our growth model. Anderson's (1982) growth rate calculations for cod were length- rather than age-structured, but our estimates of growth rate from his data were consistent with those that he estimated

for Flemish Cap. Laboratory estimates of growth rate do not necessarily reflect those obtained in the field, but in the case of Laurence's (1981) cod and haddock data, they do. Similarly, using the temperatures and ages reported by Ellertsen et al. (1981), our predictions of cod length at ages of 30–50 d were consistent with those (± 10%) actually measured in two of their three enclosures; their third, high-food density enclosure supported growth rates considerably higher than those predicted by our model. Therefore, we conclude that the age- and temperature-based growth model developed here accurately reflects the growth of larval cod and haddock over a broad range of environmental conditions, but requires modification if it is to deal with extended, anomalous food conditions. Such conditions were not encountered in seven independent larval collections in the Gulf of Maine.

General Discussion

Process-oriented growth models derived from experimental results serve a useful function as vehicles for hypothesis testing. However, studies reporting the growth of wild marine larvae have made almost exclusive use of simple age–length regressions, in apparent disregard of the more sophisticated models developed elsewhere (Bolz and Lough 1983; Beckman and Dean 1984; Nishimura and Yamada 1984; Walline 1985; Leak and Houde 1987). This situation reflects not so much the inapplicability of the alternative models, as the difficulty associated with their parameterization. Parameters are particularly difficult to estimate for terms associated with feeding and behaviour. Yet, in addition to age, feeding and temperature are the two variables most influential in determining larval growth (Vlymen 1977; Laurence 1978; Ellertsen et al. 1981; Laurence et al. 1981; Taniguchi 1981; Buckley 1984; Crecco and Savoy 1985). As a result, age–length regressions perform well as growth descriptors for a specific study, but lack applicability to other water masses, seasons, and populations.

In this paper, we hope to have bridged some of the gap between theory and application, through presentation of a generic larval growth model with a number of advantages over existing formulations. The advantages include: (1) conceptual soundness; the influence of age and temperature upon growth rate is well documented in both the theoretical and the empirical literature; (2) ease of parameterization; age-structured data can now be routinely collected through otolith microstructure techniques in a wide variety of species. Temperature data are easy to collect, either through hydrographic sampling or remote sensing observations. Since foraging data are difficult both to collect and to interpret, a feeding term has intentionally been omitted from the model; and (3) the potential for application of the model to a wide variety of environmental regimes, populations, and even species.

The robustness of any model will inevitably depend upon the nature of the inherent assumptions, and how well they are met. In this study, the assumption that otolith microstructure examination provided an accurate index of age was tested both through validation experiments and tests for inadequate resolution of narrow increments. The former were consistent with previous reports of daily increment formation in larval cod (Radtke and Waiwood 1980; Bergstad 1984; Dale 1984) in that increments formed daily in all but the early larval stage; the resolution limitations of light microscopy were almost certainly responsible for the poorer increment–age correlation among the youngest larvae. Age underestimation of the Gulf of Maine larvae was less than or equal to the magnitude of that in the laboratory, implying a minimal bias. However, the bias would be expected to be more severe in slower growing populations (Campana et al. 1987).

A second model assumption was that sea surface temperature (SST) adequately characterized the temperature environment of the larvae. Cod and haddock larvae are generally concentrated in the upper 30 m of the water column, above the thermocline (Tilseth and Ellertsen 1984; Ellertsen et al. 1984; Fridgeirsson 1984), where SST adequately reflects the temperature regime. Of course, neither day-to-day temperature anomalies nor small scale spatial variations are reflected in the smoothed temperature record used here. However, given the fact that the drift path of individual larvae was also unknown, the temperature model provided a useful integration of temperature at the daily level.

The final assumption concerned the validity of the model formulation. Yet the empirical basis for a growth–temperature interaction in cod and haddock larvae is so strong that only the omission of such a term should have to be justified. The advantage of incorporating the temperature term at the daily level was the elimination of the need for broad estimates of the mean temperature experienced by a sample of larvae. While a posteriori tests for temperature effects have been successful in some instances (Crecco and Savoy 1985), there have been other studies where the explicit incorporation of a temperature term in the growth model may have proven more effective (Methot and Kramer 1979; Jones 1985; Walline 1985; Leak and Houde 1987). A secondary benefit of the temperature term was the apparently-reduced requirement for a feeding term. While an explanation for this is not yet clear, feeding effects upon growth should become evident in the model residuals, thus providing an index of relative food availability through the study period.

Acknowledgements

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Biological Model of Fisheries Production Based on Physiological and Ecological Scalings of Body Size[1]

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Earlier ecological studies showing regularity in the relationship of certain indices of production to body size are used to develop a predictive equation of fish production on a year to year basis, with biomass and body size as independent stock variables. The prediction system makes use of the observed regular adjustments of local biomass density with body size and the parallelism of the functional relationships of production and biomass with body size both between and within stock cohorts. The method obviates the need to invoke assumptions of population equilibrium. The model is applied to three data series for individual species exploited by commercial fisheries on the Scotian Shelf. The results suggest that despite the vagaries of population sampling, ecological information can provide practical estimates of the production potential of fish stocks.

Des études écologiques antérieures, qui montraient une régularité des rapports entre certains indices de production et la taille corporelle, servent à mettre au point une équation de prévision de la production de poisson pour une année, la biomasse et la taille corporelle étant des variables indépendantes du stock. Le système de prévision utilise les ajustements normaux observés de la densité de la biomasse locale selon la taille corporelle et le parallélisme qui existe entre les rapports de production et de biomasse avec la taille corporelle entre des cohortes et à l'intérieur d'une même cohorte du stock. Il n'est pas nécessaire de formuler des hypothèses concernant l'équilibre des populations avec cette méthode. Le modèle est appliqué à trois séries de données d'espèces individuelles exploitées commercialement sur le plateau Scotian. D'après les résultats, malgré le caractère aléatoire de l'échantillonnage des populations, les données écologiques peuvent fournir des estimations pratiques du potentiel producteur des stocks de poissons.

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Management models of fisheries are designed to provide an estimate of production or yield from a population. Current biological models generally consider the exploited populations of particular species as measurable stock biomasses in a specific area. In these models, biomass of the stock is often characterized by a given age–length relationship and a numerical age structure resulting from the balance of production processes which are described by the reproduction, growth, and mortality rates. In the short term, estimates of the level of sustainable yield will vary with stocks and with secular changes in these rates. However, the major independent variable for use in yield prediction is the stock biomass or abundance index. Usefulness of these models depends mostly on the accuracy and timeliness of the biomass estimates.

Recent observations by Dickie et al. (1987a) suggest that density of the biomass in any area is dependent on the community structure that is reflected in body sizes of the constituent organisms. Hence biomass and body size taken together should provide a predictor of production, provided the size information is interpreted appropriately in relation to the physiological and ecological scaling factors underlying energetic processes. In this paper we propose that these general observations form an adequate basis for an alternative practical methodology for directly predicting current production and yield. The parameters of production that we develop are based on deductions from general ecological theory. We verify that this direct method of estimation is applicable at the species or stock level, and report here on a preliminary application to data on commercial species from the Scotian Shelf. Where the assumptions of conventional models can be shown to hold, the biological parameters derived from the body-size scalings of production improve the precision of estimates of production and yield from commercial species. Where the assumptions fail, the empirical parameters could be used to revise the models.

Ecological Considerations

The two-fold dependence of biological production on physiological and ecological processes at various body sizes needs to be considered in two parts. At the level of the physiological scaling it has been recognized for many years that production, by which we mean the total tissue elaboration, including both gonadal and somatic body substance (Mann 1969), is dependent on metabolic (physiological) rates of individual organisms and is reflected in the well known allometric relationship of metabolism to body mass (Peters 1983; Platt 1985). As a result of the relationship between production (P) and biomass (B), it follows that in natural communities average production differences

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among groups of organisms of different average body mass are indexed by the slope of the normalized biomass spectrum (Platt and Denman 1978; Sprules and Munawar 1986). However, while for particular ecosystems the resulting biomass to body size relationship may use plankton data to provide a more precise estimate of the level of fish production than did earlier more general studies (Moiseev 1969; Ricker 1969; Ryther 1969), it is clear from the low precision of the empirical relations that refinements of this overall scaling are required if the results are to be used for practical purposes (Paulik 1971; Leach et al. 1987).

On the smaller, practically important scales of production processes, such as production of particular types of species, a set of density (ecological) relations controls the dynamics of populations. In identifying and measuring the effects at this secondary scaling level, Dickie et al. (1987a) made use of the demonstration by Humphreys (1979) that within quasi-taxonomic subgroups of organisms, such as large invertebrates, fishes or mammals, production efficiency measured as the ratio of production per unit area (P/A) to respiration per unit area (R/A) is a constant. That is, within these subgroups, P/R is independent of body size or of the absolute levels of P and R in the samples. Comparison of Humphreys' (1979), Banse and Mosher's (1980) and other findings on ecosystems and species, demonstrates that this secondary allometric scaling reflects the fact that within the subgroups an adjustment of population density with body size becomes necessary in order for individual organisms to satisfy their food requirements. The ubiquity of the expression of these energy requirements in the apparent spacing of organisms seems to account for the stability of the production indices calculated by Humphreys (1979) in relation to body mass from over 250 independent experimental studies of populations of different species from both fresh and marine waters, from aquatic and terrestrial environments, ranging in size from microorganisms to large mammals, and applicable to modes of feeding ranging from filter feeders and grazers to carnivores.

It follows from these observations that changes in total abundance or biomass of a species, whether resulting from various environmental and biological factors affecting general productivity, or from vissicitudes in the reproductive ability of populations to exploit environmental opportunity, must be expressed at the local level in terms of regular density changes in relation to body size. That is, changes in abundance of species must be expressed primarily as changes in the degree of occupancy within the boundaries of their potential habitat. Given the remarkable stability of the food–energy relationships, there would appear to be an opportunity for extrapolation of observations on the energy dynamics of natural populations to management models. Such models would invoke the characteristic changes in biomass density to predict changes in productivity without the necessity of also invoking long-term equilibrium conditions in the producing populations themselves. In this paper we make use of the practical implications of these deductions to construct a multiple regression model to predict annual fisheries production at the improved level of detail allowed by the secondary or ecological scaling.

Physiological and Ecological Scaling of Body Size

For the purpose of establishing characteristic patterns of production, the relationship between production per unit area (P/A), resident biomass per unit area (B/A), and body mass (w) of the individual organisms which make up the biomass, can be described simply as a linear regression in logarithmic (base 10) terms. Dickie (1972) and Banse and Mosher (1980) formulated the relationship as

$$(1) \quad \log (P/B) = a + b \log w,$$

where their estimates of P/B were annual average values and w indexed relative sizes for different species. Individual body mass, w, is expressed in this paper in energetic equivalents, as kilocalories, using conversions of weight to kcal from Banse and Mosher (1980). Both P and B are annual values expressed in kilocalories per square metre.

In Fig. 1A we plot relationships for a number of large aquatic invertebrate and fish species in terms of equation (1), following Dickie et al. (1987a) who utilized a wider set of observations than is employed here. Fig. 1A is based on a selection of aquatic species which have been studied in detail in different areas, including marine benthic, and freshwater and marine pelagic

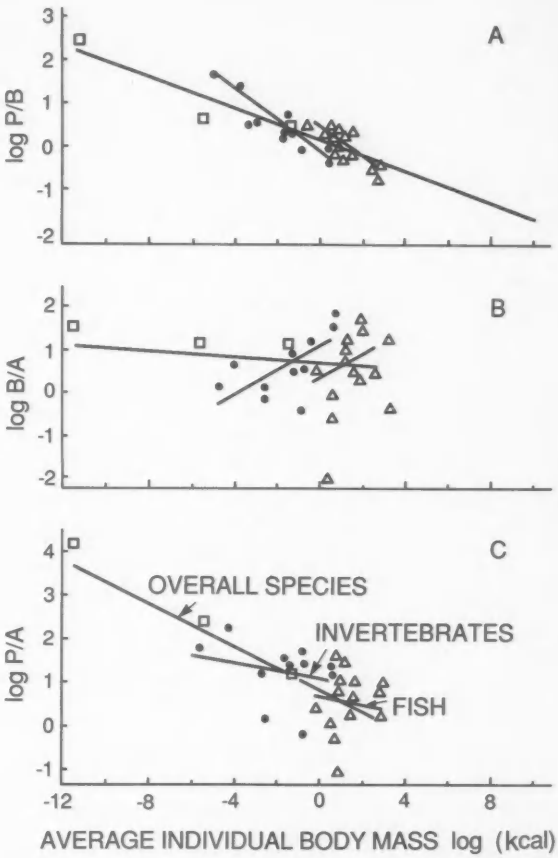

FIG. 1. Relationship of average individual body mass at age of first maturity and the various production parameters: (A) production to biomass ratio, (B) biomass density, and (C) production density, for individual species. Data on large invertebrates (●) and fish (Δ) are from Banse and Mosher (1980) and Humphreys (1979). Data from Schwinghamer et al. (1986) (□) are averages for three aggregated classes of benthic organisms: bacteria, meiofauna, and macrofauna. Lines are drawn for the overall regression and for within subgroup regressions.

TABLE 1. Coefficients for regression equations relating production parameters P/B, B, and P to body mass, w, fitted to data points on fish and invertebrate species reported by Humphreys (1979), Banse and Mosher (1980), and Schwinghamer et al. (1986)

Scaling	Data	a		b		r^2
		$\log P/B = a + b \log w$				
(A) Physiological	Overall species	0.21		−0.18		0.72
	SE		0.07		0.02	
Ecological	Within large invertebrate subgroup	−0.12		−0.38		0.83
	SE		0.13		0.06	
	Within fish subgroup	0.46		−0.33		0.83
	SE		0.06		0.05	
		$\log B = a' + b' \log w$				
(B) Physiological	Overall species	0.66		−0.04		0.01
	SE		0.15		0.05	
Ecological	Within large invertebrate subgroup	1.18		0.28		0.34
	SE		0.29		0.13	
	Within fish subgroup	0.21		0.25		0.04
	SE		0.48		0.33	
		$\log P = a'' + b'' \log w$				
(C) Physiological	Overall species	0.88		−0.23		0.43
	SE		0.15		0.05	
Ecological	Within large invertebrate subgroup	1.06		−0.10		0.05
	SE		0.30		0.13	
	Within fish subgroup	0.38		0.18		0.04
	SE		0.38		0.26	

systems. The parameters we have calculated are based on data collected by different sampling implements suited to the species distribution, body size, and behaviour, but in all cases they are expressed on a common unit area and time measurement. The calculation of the ratio of P/A to B/A results in loss of the explicit area term, but the resulting measure of productivity density, as normalized for biomass, is clearly indexed by individual body mass, whether or not the relationship is causal. The statistical data are summarized in Table 1A. The overall or physiological fitting of the relationship has a considerably lower slope ($b = -0.18$) than that representing the ecological scaling within the two major species subgroups ($b = -0.38$ and -0.33, for invertebrates and fish, respectively). While the subgroups have similar slopes they have significantly different intercept (a) values. The lower overall correlation coefficients for the overall data, compared with coefficients calculated within the subgroups, over a much smaller range of body sizes, reflects the value of the classification into subgroups.

In Fig. 1B and 1C we have recovered the original experimental data on B/A and P/A by species. They show the same double scaling with body mass that is revealed by the P/B plots, although, as might be expected, both the P/A and B/A estimates display their individual characteristic slopes with body mass. For the B/A estimates in the middle panel, the overall line is reminiscent of the biomass spectrum lines proposed for aquatic environments by Sheldon et al. (1977). That is, the overall biomass density of organisms appears to be very nearly constant from the smallest to largest sizes ($b' = -0.04$, Table 1B). A quite different picture is presented by the within species–group biomass slopes. These show high variance but positive slopes in relation to body mass ($b' = 0.28$ and 0.25); slopes that are reminiscent of the predicted trajectory of development of biomass with body size in models of individual cohort production.

The complementary relationships for P/A (Fig. 1C) show effects of scalings with individual mass similar to those observed for biomass. On the scaling of body size ranging from microorganisms to whales, production per unit area of small organisms at the base of the food chains appears to be several orders of magnitude higher than it is for the larger predatory organisms ($b'' = -0.23$, Table 1C). However, within the subgroups which Humphreys (1979) showed to have a constant production efficiency, the production that can be realized per unit area of habitat remains more or less constant, although with the high variance of the present data the exact slope with body mass cannot be determined. The line representing the fish species in Fig. 1C is plotted with the slope from the better estimated invertebrate subgroup to emphasize the similarity of within group scalings. This apparent lack of response of total production to the body size of the producing organisms is consistent with observations of the long-term constancy of annual landings of fishes from exploited natural ecosystems by Regier (1973); Regier and Hartman (1973); Sutcliffe et al. (1977). These authors have drawn attention to the relative stability of overall fisheries yield, hence production, despite long-term trends in average body size and in the species landed, and despite the fact that the changes in fishing intensity have been sufficiently large to induce these trends.

The high variation of P/A and B/A for individual species about the lines of Fig. 1B and 1C and the high standard errors of Table 1B and 1C reflect great variation in the apparent levels of species biomass and production density among the original studies. This variation may have arisen from several sources: (1) actual species abundance or rarity within an ecosystem, (2) differences in the observed ecosystems' productive capacities due to habitat characteristics, and (3) methodological or sampling differences between the various studies. The technique of expressing production and biomass in common unit area terms should eliminate most of the methodological effects, at least on the larger sampling scales. The variations must then be related to important aspects of species and ecosystem properties. The

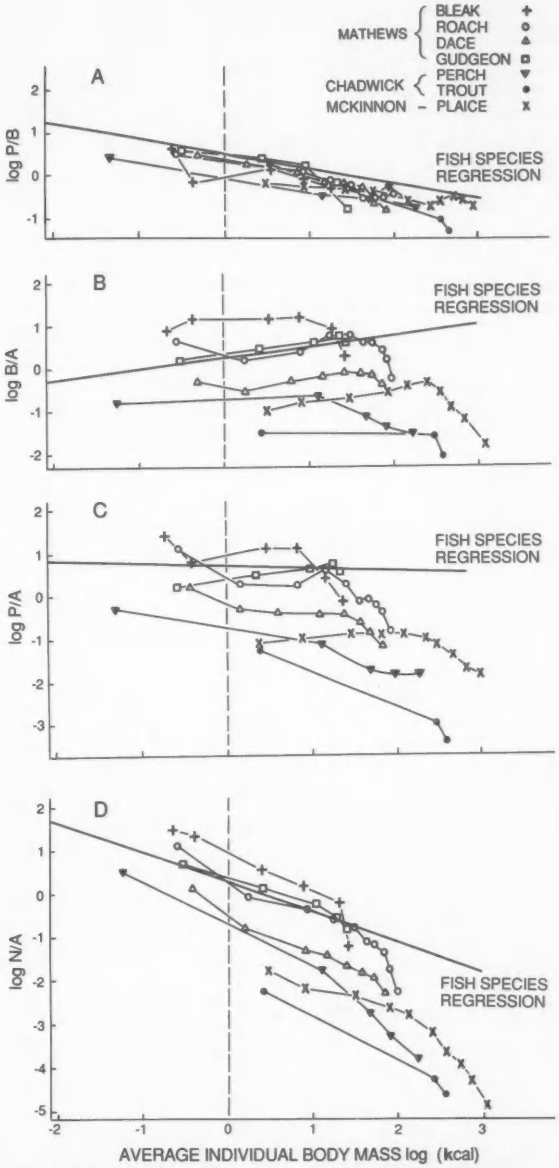

FIG. 2. Relationship (panel A–C) of the production parameters of Fig. 1 with body mass for cohorts of individual fish species. The solid straight lines are the fish subgroup regressions of Fig. 1. Panel D gives the corresponding numbers densities and within-fish subgroup regression.

fact that the resulting ratio of *P/B* in Fig. 1A has a greatly reduced standard error thus reveals an orderliness in the density relationships within ecosystem productivity levels despite possible differences in the local productive capacity of the habitat at the time the studies were conducted. That is, the population production density, normalized for biomass, appears to have also been normalized for such ecosystem differences as may have existed. It follows that differences in biomass may be used to index differences in the basic productivity among observed populations of individual species. This conclusion is integral to the development of an empirical regression equation to predict production.

Biomass and Production Between and Within Species

As indicated above, the data used to construct Fig. 1 come from several literature sources which in the reviews have generally been reduced to one average point per species. The secondary scaling as it appears in Fig. 1 is therefore, strictly speaking, a comparison between species. In the case of very short-lived animals this seems a reasonable basis for generalization. Indeed, Waters (1977) has pointed out that even if longer-lived species are included, the lifetime average *P/B* among species has low variability despite differences in the shapes of the cohort survival curves. Thus generalization based on comparisons of averages for single species on an annual production basis may capture the main features of secular productivity relations among them. For purposes of management, however, especially within fish populations, because exploitation practises may be designed in different ways to take advantage of life-history patterns of long-lived species, production throughout the cohort life history is of practical interest. This is the reason for the detailed age structuring of the dynamic-pool population models that underlie virtual population analysis (VPA) (Pope 1972). We therefore turn to an examination of productivity relationships within individual fish species.

Cohort data for several species are shown in Fig. 2A–D. The solid straight line through each panel is taken from Fig. 1 and represents the statistical fitting of the secondary or ecological scaling based on single, average points for each fish species. In this figure, we have added a bottom panel reporting numerical density which is intended to facilitate comparison of cohort data in the more conventional numerical calculation form with the biomass trends discussed here.

Each of the panels of Fig. 2 shows detailed data within three different ecosystems for the various fish species reported by Chadwick (1976); Mathews (1971); and MacKinnon (1973). The authors report on the observed population numbers, body weights, and production at successive ages observed in a temperate lake ecosystem, in the River Thames, and for a marine embayment, respectively. We show for each species one observation point per age class. Since growth tends to slow with size and age, the points for larger body sizes tend to be closer together. Several important features of these data directly reflect on their interpretation and use in models of fisheries production and yield.

First, we note that the trends in biomass, production, or numbers density within individual species (Fig. 2B–D) tend to parallel the between species lines throughout the first half of their life span. Beyond this, in all of the bottom three panels, there is a downward hook-shaped trajectory with increasing size. As expected, this downward trend is more abrupt in terms of weights or mass than it is in numerical terms. It is of importance however, that within species the trajectories for biomass and production are so highly correlated that the log *P/B* ratio for each of them in Fig. 2A exhibits a simple straight line relationship with body weight throughout the entire life history. In addition, the variation between individual species and ecosystems is very much reduced by the ratio calculation, as was noted for the between species statistics for Fig. 1 and Table 1.

The numbers density plot in Fig. 2D is based on the original sampling by size and number. As was found by Damuth (1981) for densities of grazing mammals, these observational data on average numbers and sizes for various fish species show that over most of its course the relationship between numbers density (log(*N/A*)) and log average body mass is a straight line with

a slope of approximately -0.75. Evidently the observed numbers density for fish species changes with body size in precisely the same way as has been observed for species in other environments. This is contrary to the assumption of most fisheries models that fish of different sizes and ages occupy the whole of their habitat in much the same way throughout their lives. A scaling of numbers density with $w^{-0.75}$ indicates a scaling of biomass with $w^{+0.25}$ (Dickie et al. 1987a), such as is observed in Fig. 1B and 2B within subgroups. It indicates a significant change in both numerical and biomass density with size. This increase in biomass density must result in changing catchability of the prey population by size or age if the predation mortality on them has a constant unit area basis.

It is of practical interest to note in the bottom panels of Fig. 2 the degree to which individual cohorts follow the general slope for natural populations. Uniformity between them in the early life history would suggest departure from the usual assumption of conventional fisheries models that natural fish populations, throughout most of their adult, and perhaps early lives, are subject to a constant rate of natural mortality with age. In Fig. 2D where numbers per square metre are plotted against size rather than age, the fact that the individual cohort densities initially parallel the between species density line suggests that in the production studies, natural mortality rates of the earlier ages have indeed been higher. In addition, the later downward divergence of the cohort curves from the single species line is indicative of sharp decreases in the average degree of occupancy of the habitat, a fact which is opposite to the apparent capacity of habitat to support increased biomass of larger individuals and may suggest that, in these population phases, other species may be interacting or time-sharing in the environments (Keast and Welch 1968; Tyler 1972). These two features together appear to indicate that the numbers density within cohorts changes with size and age in accordance with the general considerations of feeding opportunities and metabolic requirements discerned by Dickie et al. (1987a). They also indicate that models which assume constant parameters, may have significant bias in their output. These points need to be taken into consideration in applications.

In terms of modelling fish production and yield from data on individual species, these observations lead to three conclusions which are important. In the first place log P/B with body size (Fig. 2A), shows that precisely the same production relationships are found within as between the fish species. That is, equation (1) and the parameters in Table 1A derived from the ecological data of Humphreys (1979, 1981); Banse and Mosher (1980); and Schwinghamer et al. (1986), on individual species, apply equally to production within the cohorts of these fish species. Secondly, since the separate curves of biomass and production per unit area throughout the life span of species are not precisely parallel to the general between species lines, the calculation of production from population information within cohorts requires the specific parallel information on biomass at different average body sizes throughout the cohort life history. Thirdly, there appear to be differences in the level of the biomass and production per unit area during the latter part of the lives of cohorts even though the ratios of these two measures indicate a common production efficiency. To the extent that in each of the studies the population sampled actually utilized the total area or volume sampled, differences in the level of B/A within the species would thus be indicative of the effects of differences in utilized basic biological productivity between habitats at the time the observations are made.

It is relevant to cohort production modelling to enquire further about these differences in the levels of the individual species cohort lines. The four highest lines in Fig. 2B–D are from studies of four small species from the River Thames. It appears likely from the survey technique that the habitat area was well and uniformly sampled. Differences in B/A among these species would therefore appear to reflect differences in the effectiveness with which they utilized the total inhabited area. The two examples from Chadwick (1976), for perch and trout in a lake, are consistently below Mathews' (1971) results. This suggests that while there is consistency within studies, the apparent order of magnitude difference in biomass and production per unit area between the studies may involve a different criterion of the area of potential habitat between investigators, especially since in Fig. 2A the production ratio P/B which is normalized for area does not differ significantly among all the species. The study on plaice in a marine bay by MacKinnon (1973) is similar in B/A level to Chadwick's (1976) results but also falls within the general species lines for P/B. The study area sampled by MacKinnon is one in which it would be most difficult to assess actual area of potential occupancy relative to the area sampled. Such factors also need to be taken into practical account in applications of the method.

Multiple Regression Model

Given the forgoing considerations and the apparent stability of pattern of P/B relationships within species, it follows that the data underlying Fig. 1 and 2 can be used to predict P/A or P from information on B/A or B at appropriate intervals of average individual body mass, w, within species. Specifically, in contrast to equation 1, we may write a multiple regression equation

$$(2) \quad \log P = a + b \log w + c \log B,$$

where we agree that P and B are measured in equal area terms and we allow B to be an index of conditions of the population or production areas. That is, the conclusion that trends in production efficiencies (P/B) are stable over habitats and species may be used in this multiple regression equation to arrive at estimates of the dependent variable P from data on the independent variables w and B for any situation in which the production mechanisms underlying equation 1 are in effect.

Statistics of the fitted partial regression coefficients are summarized in Table 2A, for the combined data on invertebrates and fish species identified in Fig. 1 and Table 1. The partial slope (b) of the overall data with body mass is -0.22, a slightly larger value than given in Table 1A or by Dickie et al. (1987a), where the partial slope with B (biomass) was assumed to be 1.00. In the latter reference, additional data for other species were also included. Differences are not statistically significant.

In Table 2B are shown partial slopes with body weight by species for the individual subgroups of invertebrates and fish. These are -0.36 and -0.23 balanced by partial slope values with B of 0.94 and 0.87, respectively. From inspection of Fig. 1C it is clear that these fitted values depend heavily on the distribution of average B and w for the assortment of species and study results available. As pointed out by Dickie et al. (1987a) the values of the slope for fish species depend on the calculated averages of body mass for each species. They were derived by different reviewers from conversions between estimated size at maturity and maximum size. For general purposes of the calculation of production within various populations it is

TABLE 2. Partial regression coefficients for the regression equation
$\log P = a + b \log w + c \log B$,
calculated (A) overall species, (B) by subgroup, and (C) within individual fish species by study area, together with the average regression within species for the three fish studies.

	Coefficient							
	a		*b*		*c*		r^2
(A) Overall data	0.28		−0.22		0.81		0.97
SE		0.06		0.02		0.05	
Between species within subgroup							
(B) Large invertebrate species	−0.05		−0.36		0.94		0.92
SE		0.22		0.07		0.15	
Fish species	0.31		−0.23		0.87		0.99
SE		0.05		0.04		0.03	
Within fish species by study							
(C) Mathews (1971) (4 species)	0.22		−0.45		0.93		0.96
SE		0.06		0.04		0.07	
Chadwick (1976) (5 species)	0.09		−0.35		1.05		0.93
SE		0.26		0.05		0.15	
MacKinnon (1973) (1 species)	−0.17		−0.24		0.73		0.98
SE		0.09		0.04		0.08	
Average within fish species	0.08		−0.32		1.01		0.98
SE		0.05		0.03		0.03	

therefore more appropriate to use the average slope for the within species regressions, given in Table 2C. These within species partial slopes for the various ecosystems/studies appear to be somewhat higher than the mean slope between fish species. The average partial slopes within all fish species data, given in the last line of Table 2C, are −0.32 and 1.01 for body size and biomass, respectively. The overall correlation coefficient is 0.98.

In applying multiple regression equation 2 to data on natural fish populations, the value of the intercept of the equation (a) is of importance in scaling the results. It was pointed out earlier that investigators of the various ecosystems appear to have judged area differently, leading to differing overall estimates of biomass and production density between the various studies. The average within-species lines for the various ecosystems as reflected in Table 2C, have different intercepts depending on the particular study. Within a given ecosystem the various species levels are related to the commoness or rarity of the particular species as seen in Fig. 2B. In applying these results to species from the commercial catch we have therefore employed the estimate of average intercept derived from the 14 fish species shown in Fig. 1 for which data have been published. This intercept value is independent of the special conditions reflected by particular studies and ecosystems and is possibly closer to the requirements of general cohort production models. That is, we use the value of 0.46 from the within-fish subgroup line of Table 1A, with the understanding that the value may be subject to modification as more species and situations are studied. Using this within-fish subgroup intercept and the average within-species slopes to relate the production parameters to the variables of biomass and size, the fitted equation of the model is

$$(3)\quad \log P = 0.46 - 0.32 \log w + 1.01 \log B.$$

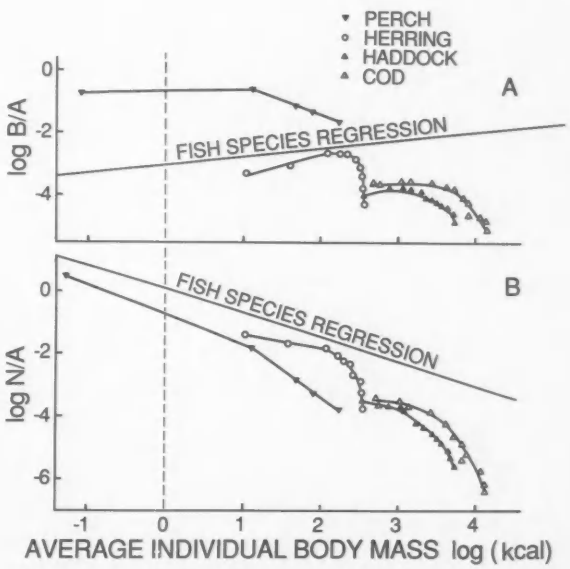

FIG. 3. Relationship of (A) biomass density and (B) numbers density to body mass, calculated from representative cohorts of cod, haddock, and herring from the Scotian Shelf. A line describing the relationships for biomass and numbers for Chadwick's (1976) perch from Fig. 2 is included. The fish species regressions are drawn with the same slopes as in Fig. 1 and 2 but scaled to a corresponding density level.

Application

An appreciation of the practical usefulness of the foregoing emerges from preliminary application to data on three of the main species exploited commercially in the northwest Atlantic: cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and herring (*Clupea harengus harengus*). Continuous standardized records of landings are available for fisheries of the

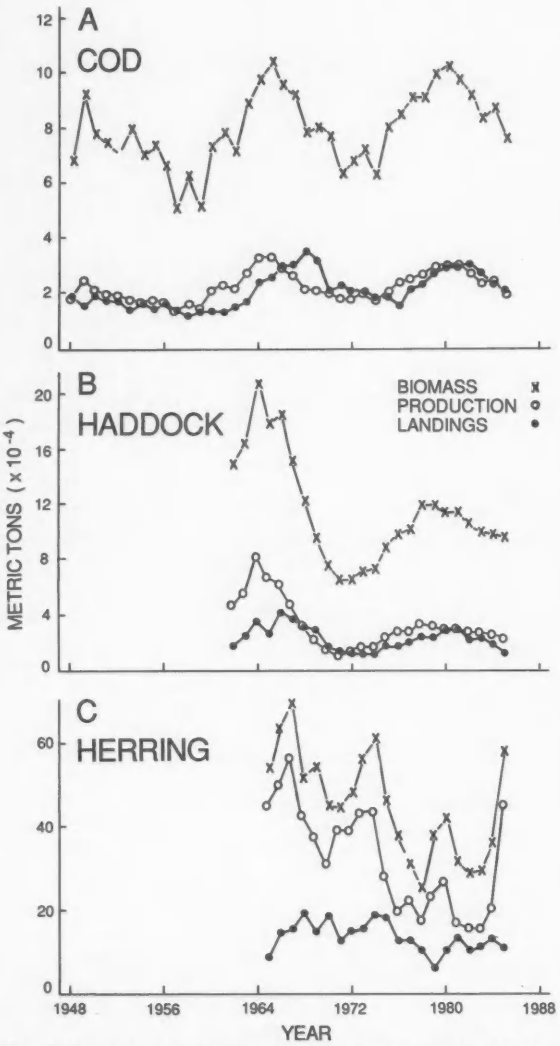

FIG. 4. Trends in annual landings, biomass, and production for three species fished on the Scotian Shelf.

Scotian Shelf since the mid 1940's. Sampling of landings for numerical age compositions and length–weight relationships, necessary to calculate biomass estimates by VPA, has depended on a number of factors. We have used the data series published in the Canadian Atlantic Fisheries Advisory Committee (CAFSAC) research documents, giving estimates of population numbers and biomass by species, ages, and years (O'Boyle and Wallace 1986; Campana and Simon 1986; Stephenson et al. 1986). For cod and haddock we use data for Northwest Atlantic Fisheries Organization (NAFO) subarea 4X. For herring we use data for NAFO subarea 4WX combined since the stocks of this species complete an annual migration cycle and are fished through both areas. Biomass estimates for cod are available from 1948, for haddock from 1962, and for herring from 1965. Each annual biomass estimate is accompanied by an instantaneous fishing mortality rate (F) calculated from the total annual landings. Population and landings data are summarized in Fig. 3 and 4 and in Table 3.

For each species we have used the published population numbers and biomass at size (ages 1+) calculated from landings data by use of the VPA methodology. In compiling these data we use an estimate of total area to calculate a relative number and biomass density. Since the species occupy an unknown fraction of the whole of the statistical areas, such a correction is biased and intended only to bring the three species somewhat nearer to a single reference standard for easier comparison of the data trajectories. The first step in application was to compare the cohort data for the three species with the general species information in Fig. 1 and 2. For a representative cohort of each species we plot in Fig. 3A, B values for B and P that have been arbitrarily scaled for comparison with Chadwick's (1976) data on perch.

The original biomass estimates were based on sampling of the commercial landings at age in conjunction with independent estimates of relative population abundance (research vessel data, larval surveys) that are used to tune the VPA output. The same data are also used to calculate an average size at age in the landings. Such data will reflect bias as a result of fishing gear selectivity by size, as well as selection in area fished in relation to the seasonal distribution patterns of the fish. It is on this account, for example, that the initial or age 1 sizes for the commercial species appear to be so large. Selectivity would undoubtedly also account in large measure for the anomalous indication in Fig. 3 that the smallest cod and haddock are of about the same size as the largest herring. Clearly the sampling does not reflect the actual average sizes of the younger age groups in the populations. This bias will result in systematic errors when these values are used in our production model, underestimating production as a result of the overestimate of average size. Although such sampling errors may create difficulties for comparisons between species or populations, they are probably relatively stable within species over the time series used here, and so we have made no attempt to correct them to values which would be closer to the biological population values.

Comparably, estimates of numbers and biomass at age are subject to biases incorporated in assumptions underlying the use of VPA. In particular, numbers-at-age derived from VPA are dependent on use of a constant level of natural mortality to characterize the entire life history, and on the accuracy of the single value chosen. Higher early natural mortality rates with size, were postulated from the P/B data by Dickie et al. (1987b). Higher natural mortalities would result in higher numbers and somewhat higher biomasses at the younger ages. Similar corrections have been suggested for a number of commercial species by Sissenwine (1985); and Daan (1987), based on very extensive sampling.

To help assess the possible importance of these known biases in the cohort data for exploited stocks, we plot on Fig. 3A and B the cohort observations for the natural unexploited population of perch from Fig. 2B and D. In Chadwick's (1976) lake study the entire population of fish species was enumerated directly and gives a more detailed reference curve than could be afforded by any calculation based on a priori assumptions. In Fig. 3A the biomass density for the exploited stocks has a higher slope than was calculated from the perch population samples at small sizes. Similarly in Fig. 3B, the calculated slope of numbers with size, at smaller sizes, are lower than in the observed perch population confirming the likely influence of bias resulting from

TABLE 3. Statistics of relationships among landed average body mass (w), biomass (B), production (P), landings (L) and fishing mortality (F) for three commercial species fished on the Scotian Shelf. B and F are as calculated from landings by virtual population analysis. P is calculated from B and w using equation (3). Statistics for L and F in columns 7, 8, and 9 are calculated in relation to P 2 yr earlier (cod and haddock) or 1 yr earlier (herring).

Column	1	2	3	4	5	6	7	8	9
species (area)	Body mass (kcal)	P/B	L/B	$r_{L \cdot B}$	$r_{L \cdot F}$	$r_{L \cdot FB}$	L/P	$r_{L \cdot P}$	$r_{L \cdot FP}$
cod (4X)	1469	0.28	0.27	0.61	0.58	0.80	0.96	0.88	0.92
haddock (4X)	1097	0.32	0.23	0.75	−0.05	0.75	0.65	0.88	0.88
herring (4WX)	86	0.74	0.30	0.45	−0.14	0.52	0.42	0.81	0.81

the low estimates of natural mortality among these size and age groups. The right hand portions of the cohort lines in both Fig. 3A and B exhibit curvatures which are steeper than characterize the unexploited populations on which the multiple regression model is based. This may partly reflect the effects of fishing mortality on the commercial populations. Without independent biomass distribution data, such as might be provided by extensive population sampling by research vessels using nets or acoustic sampling, it cannot be ascertained how much of these deviations involve unrecognized trends in mortality and how much may involve changes in catchability with age or size. Both effects, if taken into account, would make the actual trends in population densities calculated from landings closer to trends observed in the population data of Fig. 2.

Given these uncertainties respecting trends of actual densities with size within the three commercial species, application of the production equations to the detailed cohort data is unlikely to improve our appreciation of production potential of the stocks. This would require unbiassed population samples. However, both the commercial population data and the general curves show features which encourage further exploration. In the first place, the patterns displayed by the commercial cohort biomass data over years and stocks (Fig. 3A) are remarkably uniform, and follow a generally parallel course with body size relative to the species reference line. With such parallels it is reasonable to conclude that the production characteristics being displayed by the commercial species are uniform and that differences in level of productivity from year to year are adequately indexed by the changing biomass index even if the divergence of the cohort pattern from the observed species patterns indicates a biased estimate of the actual level. In the second place, the observational data on which the ecological analysis depends show that the P/B relationship with body size between species is identical with that within cohorts. Using this fact in conjunction with the parallelism we can apply regression equations from the general study to annual average biomass and body size data from the commercial sampling, assuming that the exploited species are subject to the same general laws governing the ratio of production to biomass as are the other species for which measurements have been made.

In keeping with these considerations we have compiled annual statistics of landings and of biomass for the three commercial fisheries. The results are shown in Fig. 4A–C. The changing total biomass and fished body size from each year's landings, is used as input to calculate an estimate of total annual production using equation (3).

As would be expected, the calculated biomass trends closely parallel the landings data from which they are derived, and the estimated production values parallel the level of biomass. Relations among the various statistics are summarized numerically in Table 3. In column 3 it appears that average annual landings for each species are between 20 and 30% of the estimated average biomass. Column 4 shows that annual landings and annual biomass have correlations of 0.61, 0.75, and 0.45 for cod, haddock, and herring, respectively. These biomass and landings ratios must, however, apply to species that have quite different production characteristics reflected in differences in their average body mass, w. The ratio of average P to average B for each of the three panels of Fig. 4 is given in column 2. It ranges from 0.28 through 0.32 to 0.74 for cod, haddock, and herring, respectively, a sequence which relates well to the relative average body mass data of column 1 and the corresponding general relative levels derived from the ecological relationships and portrayed by the secondary scaling of P/B for fish species in Fig. 1A.

The distinctly different turnover rates characterizing the three species helps explain anomalies in the trends of the simple regression of F, the fishing mortality rate on L, the landings, in column 5. That is, if the catchability coefficient is assumed to be more or less constant over time within each species, the estimate of F derived from the landings data should be a reflection of the changing amounts of fishing effort devoted annually to the fishery for each species. In column 5, F is positively correlated with landings for the longer lived cod but for haddock and herring, there is no significant correlation. Because landings are a result of the action of fishing mortality on the average biomass, this lack of simple relationship between L and F for such relatively stable biomass levels as illustrated in Fig. 4, is somewhat unexpected. The multiple regression of L with both F and B in column 6 shows, however, that the inclusion of biomass fluctuations does tend to improve on the simple correlations with either F or B alone. Therefore, between species, the decreasing significance of the relationship between L and F with increased P/B (column 2) shows that a direct relationship with P is involved.

The relationships among landing, mortality, and production are explored in the final columns of Table 3. The trends in the data presented in Fig. 4 show that production is related to landings. Cross correlation analysis shows that cod and haddock production has the highest correlation coefficient with landings 2 yr later, and for herring with landings 1 yr later. In column 7 we show average L/P for the three species using the indicated time lags. As suggested above, the general level of P is probably underestimated so that the calculated average L/B is too high, however the level by species is inversely related to P/B, as would be expected. Column 8 gives the correlation coeffi-

cient for production estimates with the appropriately lagged landings. The simple correlations between them are stronger than for the earlier comparison with B and F in columns 4–6. The final column of the table shows the multiple regression when F is included in the L, P relationship. It suggests that the calculated annual production of the three species is the primary determinant of the fishery yield and is the strongest available predictor in this calculation system. The lag involved between the production in 1 yr and realized landings 1 or 2 yr later provides a basis for prediction if unbiased estimates of current levels of biomass and size could be achieved in real time.

Discussion

It appears that when principles of physiological and ecological interaction underlying production are applied to biomass and body size data for commercial stocks, the predictions of production and yield are of the same level and degree of precision as are afforded by current methods of fisheries analysis. The results of this application suggest, however, that for any practically reliable management prediction system three not two orders of scaling of production processes with body size are involved, and may need to be explicitly recognized. We have, in fact, not attempted here to test the usefulness of the overall or primary, physiological body size scaling identified by Dickie et al. (1987a). Instead, we have concentrated on describing the between and within species or cohort relations about the secondary or ecological scaling. Strictly speaking, the species subgroup relationships of Fig. 1 correspond to the secondary ecological scaling phenomenon postulated by Dickie et al. (1987a). The within-species or cohort lines (Fig. 2) therefore constitute the third order scaling with body weight. It is the apparent similarity of interactions at these potentially different secondary and tertiary levels which led us to base production and yield predictions for commercial species on average parameter values for species indicated by the secondary scaling. We have no a priori information which would show that this is as precise as it could be. Indeed, because the commercial data cannot at present be shown to be free from bias, both the method of application and the results from it may be deficient. The apparent coherence of the relationships is, however, decidedly encouraging and would appear to justify more extensive study.

Of particular interest is the efficacy of using total observed biomass as an index of the level of productivity of a stock in a given area and year. Analyses of fisheries have for many years assumed a constant catchability coefficient over time for the fully exploited stocks, an assumption which implies that local densities of fish at a particular size do not change with changes in abundance. The same phenomenon is implied by the generality of the observed P/B relations with body size that are invoked here and illustrated in Fig. 1A. That is, our model implies that it is possible, at least in part, to break away from the restrictive assumptions of population equilibrium states often invoked in ecological generalization. We infer that control of biological production processes per unit area takes place on the time scaling of energy flows required to satisfy food requirements of individual organisms operating at a constant efficiency. Changes in the capacity of the environment to satisfy these requirements should be reflected in average population densities revealed by local sampling and which may be reflected in such environmental indices as average temperature or the available nutrient concentration. On this basis a measure of total biomass can be taken simply to represent the scope of the time and space measures of the production events. The apparently successful application of our methodology to the time series of annual data for commercial species occupying different environments, may also provide a demonstration of the validity of the assumption that the catchability of a species is independent of its abundance.

It remains to be determined whether or not within a species, a constant catchability assumption can be justified for the fully recruited fish sizes or ages of a single cohort. It was pointed out earlier that the lack of correspondance between the cohort densities calculated from the data for commercial species and those derived from observed natural populations indicates a potential source of bias which adversely affects application of our production equation. No extensive test of the magnitude or statistical significance of the trends in calculated cohort densities can, in fact, be undertaken at the present time. There seems to be no a priori reason why detailed cohort data, rather than cohort averages within years should not be employed in the regression model and be expected to lead to improved estimates. In fact, as suggested above, it may even be that improved cohort trajectories will emerge from a closer study of the natural mortality and catchability trends implied in our comparisons. However, at present we can only suggest that such procedures be examined in the future in relation to sampling information from unbiased survey data. Of particular relevance in the present context would be the information on local density by body size that may emerge from surveys using appropriate acoustic detection techniques.

In making comparisons between our system of production estimates and conventional yield calculations we have used the reported landings and their ratio to biomass and total biological production as a point of reference. Thus for example, in our calculations, the ratio of landings to production is lower for herring than it is for haddock or cod, reflecting the well known fact that herring devote a relatively larger fraction of their annual production to reproductive growth than do many other fish species. The dependence of the relationship between reproductive and somatic growth to body size and to a density dependent term, comparable with our biomass density, was discussed by Ware (1980), who suggested that there is a regularity in the energetics which may be of practical value in studies of recruitment. We do not go further here than to point to the desirability of additional study along these lines in any attempt to develop a specific production to yield relationship. In this paper, considerations of this kind would be relevant to judging the importance of differences in the average landings to production ratios between herring, haddock, and cod. It may even appear that there are practically important differences in the ratios of the components of production within species where there are changes in fishing patterns or abundance levels. For present purposes, where we are using single annual production values for species, comparing and predicting changes in average annual levels within species makes the not unreasonable assumption that at existing levels of fishing effort and biomass, the ratio of the production components has not exhibited significant trends.

In comparing the performance of the three commercial species it is relevant to take account of the fact that quota controls were introduced to the fisheries during the 1970's. The time series of data do not show that there has been a measurable change in the average landings–biomass or landings–production ratios since regulations were instituted. However, it is symptomatic of difficulties in management to note that between species, the more productive haddock and herring show a low,

insignificant correlation between landings and the best available measure of fishing mortality (F). The fact that landings of cod, which has a relatively low P/B, on average equal the quota, haddock landings tend to fall short of the quota, while herring landings are consistently high, appears to reflect the increasing dependence of fishing success on the replacement rate rather than on any particular measure of average biomass density. This is reflected in the general improvements in correlations of landing with production despite the fact that we have not developed an explicit yield–production relationship.

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Origin and Dispersion of Larval Herring (*Clupea harengus*) in Coastal Waters of Eastern Maine and Southwestern New Brunswick

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Repetitive surveys of larval herring (*Clupea harengus*) were undertaken in coastal waters between Mt. Desert, Maine and Saint John, New Brunswick to define the location, timing, and extent of spawning and the distribution of larvae. Three surveys during September and October 1986 showed two separate areas of larval dispersal. The easternmost stations contained low densities of large larvae which were assumed to be part of the annually occurring larval aggregation off Nova Scotia. High densities of small larvae west of Grand Manan indicated that spawning in this area was confined to a small area southwest of Grand Manan and along the eastern Maine coast. This unique larval distribution confirms the autonomous nature of the eastern Maine–Grand Manan spawning group. Back calculation indicated hatching times between late July and the middle of October, but most of the larvae taken in the survey hatched in August and September. The larvae west of Grand Manan occurred within a well mixed water mass containing a characteristic neritic zooplankton community. Some larval herring remained near the spawning ground over a 2-mo period, while others dispersed west along the coast.

Des études répétées des larves de hareng (*Clupea harengus*) ont été réalisées dans les eaux côtières entre Mont Desert au Maine et Saint-Jean au Nouveau-Brunswick afin de déterminer l'emplacement, la période et l'ampleur de la ponte et de la distribution des larves. Trois études réalisées en septembre et en octobre 1986 ont montré que les larves se dispersaient en deux régions distinctes. Les stations les plus à l'est ont présenté de faibles densités de grosses larves, que les auteurs ont supposé faire partie du regroupement annuel de larves qui se produit au large de la Nouvelle-Écosse. Les densités élevées de petites larves, observées à l'ouest de Grand Manan ont montré que la ponte dans cette région a été confinée à une petite zone située au sud-ouest de Grand Manan et le long de la côte est du Maine. Cette distribution particulière des larves confirme la nature autonome du groupe de Grand Manan-côte est du Maine. Des calculs ont montré que la période d'éclosion se situait entre la fin de juillet et la mi-octobre, mais la plupart des larves prélevées dans le cadre de l'étude ont éclos en août et en septembre. Les larves observées à l'ouest de Grand Manan se trouvaient dans une masse d'eau bien mélangée, renfermant une communauté de zooplancton néritique caractéristique. Certaines larves sont demeurées près de la frayère durant 2 mo, alors que d'autres se sont dispersées vers l'ouest le long de la côte.

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Juvenile Atlantic herring (*Clupea harengus*) in coastal waters of eastern Maine (U.S.A.) and southwestern New Brunswick (Canada) are transboundary and support valuable fisheries in both countries. Landings have recently declined, raising questions about the continued viability of the fisheries and emphasizing the need to understand the stock dynamics of herring. The stock origin of these fish is still uncertain. Several populations may contribute, but there always has been some spawning along the Maine coast and around Grand Manan Island, New Brunswick and this undoubtedly supplies part of the recruitment to the juvenile fishery. The widespread spawning south of Grand Manan and along the Maine coast that was reported in the past (Moore 1898; Bigelow and Schroeder 1953; Huntsman 1953) is now confined to smaller areas in eastern Maine, but still occurs there in a constant and predictable manner (Stevenson 1984). Herring probably home to the spawning sites in eastern Maine as they do elsewhere (e.g. Newfoundland waters, Wheeler and Winters 1984).

In September and October 1986 we conducted three larval surveys in coastal waters of eastern Maine and southwestern New Brunswick to answer two questions concerning the relationship between the local spawning stock and the juvenile populations in the area. First, how extensive is the spawning in time and space? Other larval surveys in the western Gulf of Maine and Bay of Fundy (Iles et al. 1985; Grosslein 1987; Smith and Johnson 1986; Graham et al. 1984; Townsend et al. 1986) were either on large spatial scales or covered only a portion of the area of interest, so that the extent of spawning in the coastal transboundary area is still unknown. Second, what is the fate of the larvae? Whereas observations on spawning areas off

southwest Nova Scotia led Iles and Sinclair (1982) to the conclusion that larvae remain in the area of spawning beds for considerable lengths of time, studies of herring larvae in eastern Maine waters have concluded that there is transport of larvae in a westerly direction away from the spawning areas (Graham 1982; Townsend et al. 1986). The objective of our research was to document spawning locations and follow the movement of early larvae by repetitively sampling a block grid of stations over potential spawning grounds.

Methods

We conducted three larval survey cruises during September and October 1986 along the coastal shelf between Mt. Desert Island, Maine and Saint John, New Brunswick. Fifty-five sampling locations were scheduled for each cruise (Fig. 1); 50 stations were completed during September 2–12, 55 during September 22–October 1 and 50 during October 20–30.

Biological data were obtained during daylight hours only, using a 61-cm bongo frame mounted with white 0.333-mm mesh nets, hard plastic codend buckets and flowmeters (General Oceanics Model 2030). Standard oblique bongo hauls of a minimum 10-min duration were deployed to 5 m off bottom at 50 $m \cdot min^{-1}$ and retreived at 20 $m \cdot min^{-1}$ using a meter block (General Oceanics) with 1/4-inch wire. Samples were fixed in 5% formalin and seawater buffered with marble chips.

Hydrographic data were collected at each station. Surface samples for salinity and temperature measurements (accurate to 0.1°C) were taken from a bucket. Bottom salinities and temperatures were obtained with Niskin bottles and reversing thermometers (accurate to 0.01°C). Salinities were measured using a Guildline Model 8400 salinometer.

In the laboratory, all fish larvae from the port, 61-cm bongo net were counted and a representative subsample of up to 100 herring larvae per station were measured (standard length) to the nearest millimetre. An aliquot of 5 mL was removed by pipette from the remaining sample while thoroughly mixed in 500 mL of seawater. *Calanus* spp. and other copepods in the aliquot were identified and counted to define community structure.

Results

Spatial Distribution of Larvae

The distribution of larvae (Fig. 2) shows that major aggregations (1–15·m^{-3}) occurred southwest of Grand Manan Island and along the eastern Maine coast. These larvae were generally less than 13 mm and belonged to distinct size modes. There was a paucity of larvae in the waters immediately north and east of Grand Manan and also south of Grand Manan beyond the 100-m isobath, so that the larvae east of Grand Manan, which were much less abundant and generally larger, appeared to be spatially separated from those west of Grand Manan. The larvae east of Grand Manan had a center of concentration off Saint John, N.B.

The polymodal nature of the length-frequency distributions of larvae at stations west of Grand Manan provided rationale for dividing the distribution into several length groups (Fig. 3). The analysis of length-frequency distributions described by Macdonald and Pitcher (1979) and Macdonald (1987) confirmed that the larvae were distributed around the length intervals; 4–6, 7–12, and 13+ mm standard length. The length groups correspond to larval ages of 0–7 d (yolk sac larvae) 8 d–1 mo and greater than 1 mo, respectively, by assuming a length at hatching of 5 mm (Bigelow and Schroeder 1953; Sindermann 1979) and an average growth rate of 0.24 $mm \cdot d^{-1}$ (as determined in this report). The spatial distributions of each size group for each cruise are shown in Fig. 4.

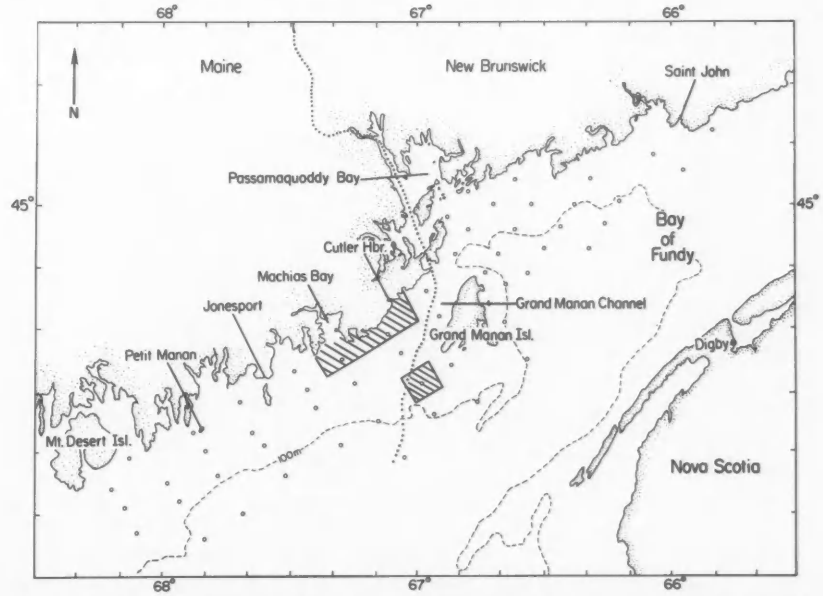

FIG. 1. Location of sampling sites along the coast of eastern Maine and southwestern New Brunswick during the Canada/USA larval herring survey; September and October 1986. Shaded areas indicate approximate locations of spawning.

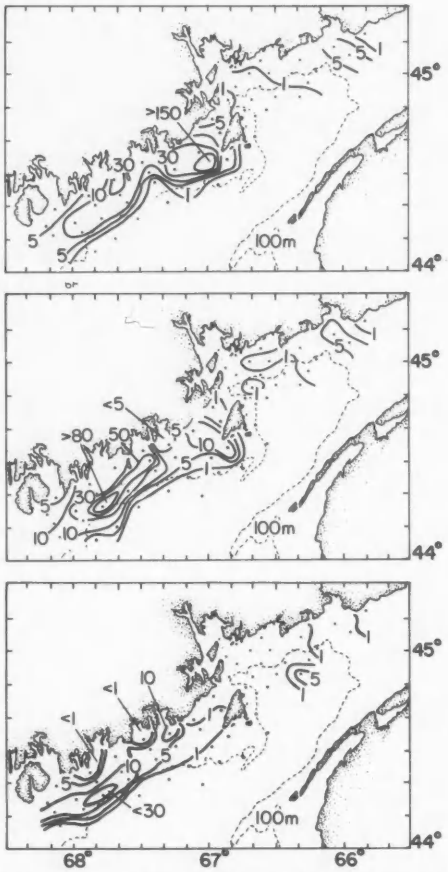

FIG. 2. Synoptic maps of larval herring distribution (No.·10 m^{-3}) during three surveys in coastal waters of eastern Maine and southwestern New Brunswick. Top; Sept. 2–12, middle; Sept. 22–Oct. 2, and bottom; Oct. 20–30, 1986.

Recently hatched larvae (4–6 mm), some having yolk sacs, must have been only a few days old and therefore would indicate nearby spawning sites (Fig. 4). They were observed only during the first two cruises and occurred in two relatively small areas, one about 6 miles southwest of Grand Manan on the first cruise and another just off the coast of Maine between Cutler Harbor and Machias Bay on the second cruise. The density of newly hatched larvae observed southwest of Grand Manan was about 12·m^{-3} which was similar to the density of larvae on the larger spawning grounds off southwest Nova Scotia (R. L. Stephenson, M. J. Power, unpubl. data).

Unfortunately, one station off Cutler Harbor and one off Machias Bay were not sampled on the first cruise, but additional evidence for spawning in that area was provided in a concurrent study by D. K. Stevenson (D. K. Stevenson, pers. comm.) who reported information by fishermen and direct observation of egg beds at five locations in eastern Maine between July 29 and Sept 22, 1986. The repetitive occurrence of 7–12 mm (8 d–1 mo of age) larvae southwest of Jonesport during our cruises raises the possibility that spawning sites may have extended farther west. However, no 4–6 mm larvae were taken west of Jonesport, nor have egg beds been reported in the area so we assume those larger larvae dispersed westward from the spawning grounds identified above.

The 7–12 mm larvae constituted the dominant size-group west of Grand Manan during each cruise, although they were obviously not hatched at the same time. The length distribution of these larval patches had sharp modal peaks between 8 and 10 mm. The temporal distribution of the larvae indicated movement from the immediate spawning sites, but most remained within the study area for at least 1 mo. The 7–12 mm larvae taken in the first two cruises were generally aggregated into two patches, one immediately southwest of Grand Manan and the other southwest of Jonesport (Fig. 4). The concentration of these larvae was higher in the patch southwest of Grand Manan in the first cruise, but was higher in the patch southwest of Jonesport in the second cruise. There were virtually all concentrated southwest of Jonesport during the third cruise.

The larvae in the 13+ size-group were present in much lower densities, but still occurred in patches both west of Grand Manan and in the east, off Saint John (Fig. 4). The greatest density occurred to the southeast of Jonesport during the second cruise. Most of these larvae were between 13 and 18 mm, or between 1 and 2 mo old, at the estimated average growth rate (0.24 mm·d^{-1}).

Estimates of Larval Growth and Back Calculation of Hatching Dates

The polymodal nature of the length frequencies for larvae west of Grand Manan allowed us to estimate the growth rate for two groups of larvae (B and C, Fig. 3). One estimate was made by comparing modal lengths of larvae in the 7–12 and 13+ mm size groups from Group B and another was made comparing modal lengths of larvae in the 4–6, 7–12, and 13+ mm size groups from Group C. We felt that Groups B and C contained larval patches which showed related patterns of dispersal between cruises (Fig. 4). With this method we estimated larval growth west of Grand Manan to be 0.28 mm·d^{-1} for Group B and 0.20 mm·d^{-1} for Group C (Table 1). We used an intermediate rate of 0.24 mm·d^{-1} as an average estimate of growth during the sampling period.

Our growth rate estimates of 0.28 mm·d^{-1} for Group B and 0.20 mm·d^{-1} for Group C compare well with those of Townsend and Graham (1981), who used the daily growth increments of larval herring otoliths from the Sheepscot estuary to determine that the larvae grew at a rate of 0.28 mm·d^{-1}. They also compare well with other estimates of larval growth rates in the Northwest Atlantic, as summarized in Townsend and Graham (1981) most of which varied between 0.20 and 0.28 mm·d^{-1}. We were able to estimate the approximate time of hatching for larvae within individual patches by identifying their modal lengths in each significant patch (Fig. 4) and then applying our estimated growth rates to calculate the number of days back to 5 mm. The hatching times of larvae in the patches are given in Table 2.

Hatching apparently began in late July and continued until about the middle of October, but most of the larvae taken in the survey cruises had hatched in August and September. The larvae in Group A appear to have hatched in July but we observed them in our samples only as 13+ mm larvae in Cruise 1 (Fig. 4). The evidence for hatching as early as late July in 1986 is supported by the report of D. K. Stevenson (D. K. Stevenson, pers. comm.) that herring eggs were observed on lobster gear at about that time in some areas of eastern Maine.

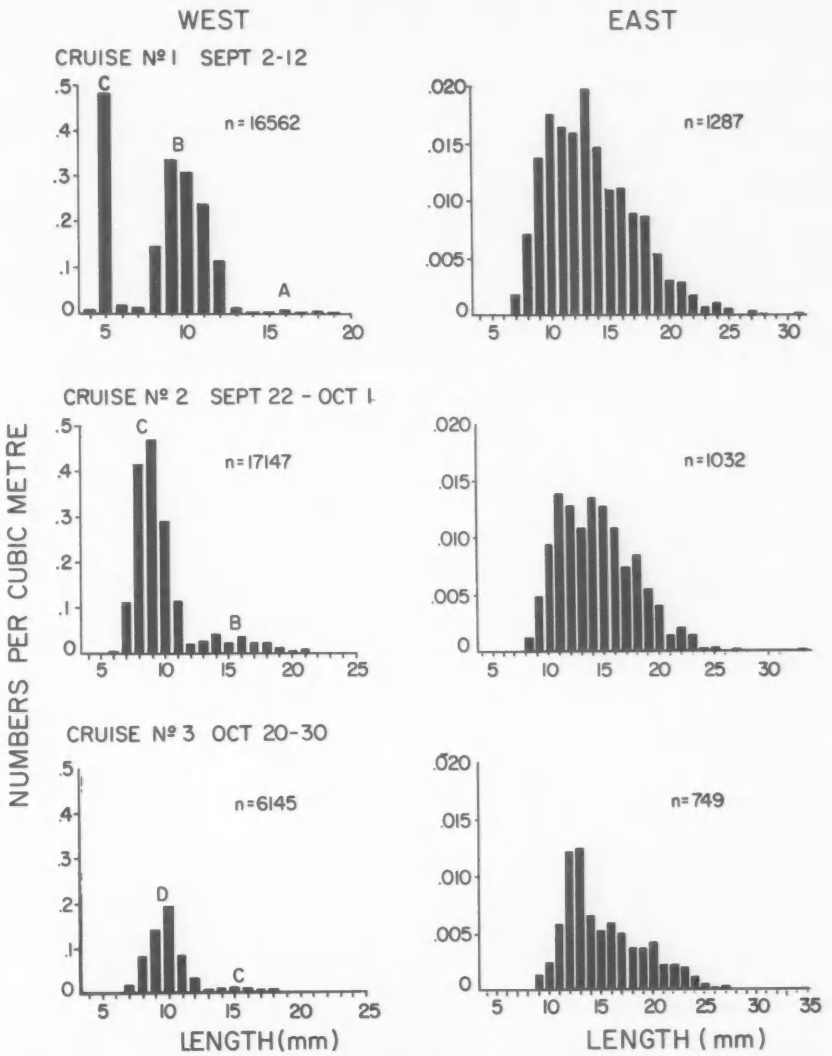

FIG. 3. Length frequency distributions ($n \cdot m^{-3}$) for the sum of all sets of herring larvae taken at stations east and west of Grand Manan during the three surveys of coastal waters of eastern Maine and southwestern New Brunswick in September and October 1986. Letters denote groups of larvae referred to in Table 1 and text.

The larvae in Group B hatched in August and we observed them as 7–12 and 13+ mm larvae in Cruises 1 and 2. Most larvae in Group C hatched in early September and we observed them as successively larger size groups throughout the sampling period. Group D hatched in early October between Cruises 2 and 3 and we only observed them as 7–12 mm larvae in Cruise 3.

Movement and Mortality of Larvae

The only confirmed spawning sites were located in coastal waters between eastern Maine and Grand Manan (Fig. 1), where all recently hatched larvae (4–6 mm) were located. When the larvae appeared to move they did so in a southwesterly direction along the Maine coast, at least as far as Mt. Desert, but not northeastward into the Bay of Fundy or eastward out into the open Gulf of Maine. The pattern of movement can be more precisely defined by examining the spatial relationships of individual larval patches along the diagonal in Fig. 4 (e.g. patches C1, C2…C5) and by relating the patches on the basis of individual hatching dates (Table 2).

The C group of larvae which hatched in early to mid-September, showed some westward dispersal (C1-C2-C4) and some retention near the spawning grounds (C1-C3-C5). The hatching dates of this last series of patches were strikingly similar (first week in September) and were found as identifiable aggregations in each of the three cruises in successively larger size categories. The A and B groups, which hatched in late July and in August, respectively, showed very little westward movement. The larvae in patches A1, A2, and B3, in particular, were large enough to have remained in the area for up to 2 mo. Group D,

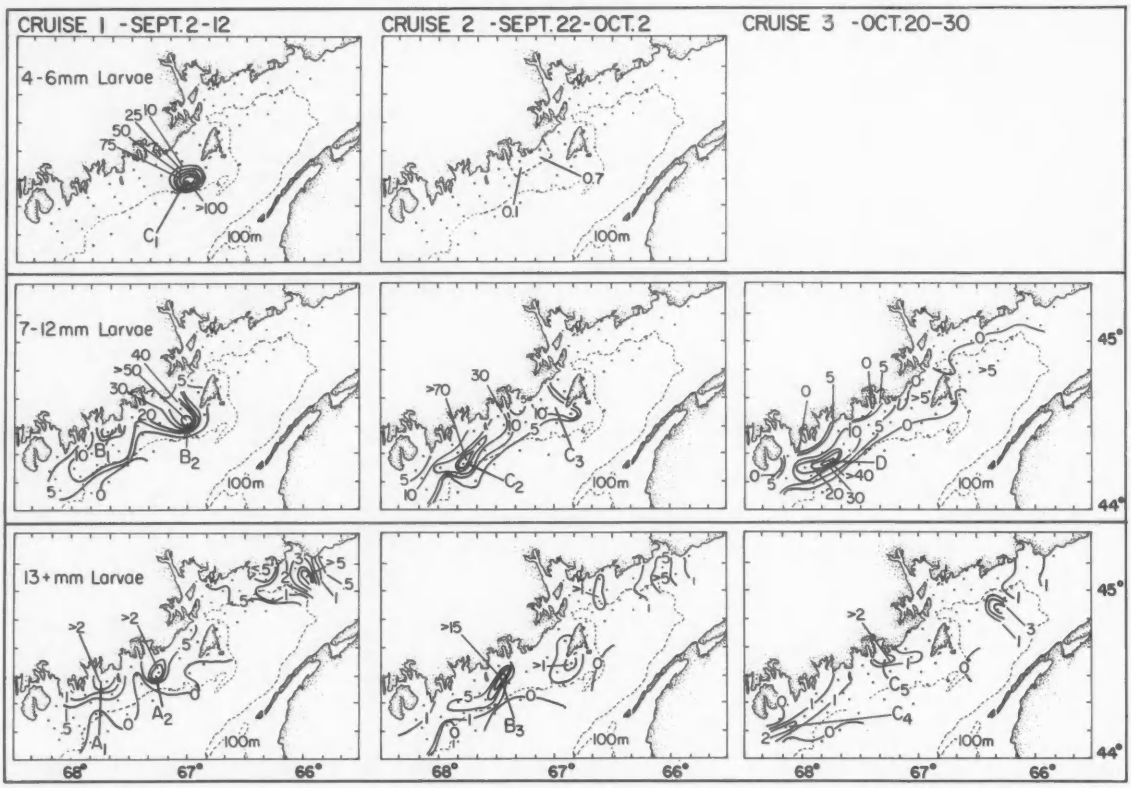

FIG. 4. Spatial distribution of three size groups of herring larvae (No.·10 m^{-3}) on three successive surveys of coastal waters off eastern Maine and southwestern New Brunswick during September and October 1986. Letters and numbers denote patches referred to in Table 2 and text.

TABLE 1. Growth estimates from modal lengths of larval cohorts

	Group B	Group C
Increase in modal length	6 mm	10 mm
Time between mean sampling dates	21 d	49 d
Estimated growth rates	0.28·d^{-1}	0.20·d^{-1}

TABLE 2. Approximate ages and hatching dates of larvae of similar size within a patch based on modal lengths and an assumed growth rate of 0.28 mm·d^{-1} for Groups A and B and 0.20 mm·d^{-1} for Groups C and D.

Larval patch	Date observed	Larval size (mm)	Age (d)	Date of hatch
A1	9/4	16–19	39–50	7/16–7/27
A2	9/5	15	36	8/01
B1	9/4	10	18	8/16
B2	9/6	9	14	8/23
B3	9/25	13–18	29–46	8/10–8/27
C1	9/6	5	0	9/06
C2	9/30	8	15	9/15
C3	10/1	10	25	9/06
C4	10/26	13–18	40–65	8/22–9/16
C5	10/21	15	50	9/01
D	10/26	8	15	10/11

TABLE 3. Larval herring abundance and mortality rate (instantaneous and percent per day) calculated from cohorts observed in successive cruises.

Patch	Size (mm)	Cruise No.	Total number of larvae	Interval (d)	Mortality/day Z	Mortality/day percent
C1	4–6	1	1.41×10^{11}			
C3	7–12	2	4.20×10^{10}	20	0.06	3.5
C5	13+	3	5.66×10^{9}	28	0.05	3.0
B1+B2	7–12	1	1.61×10^{11}			
B3	13+	2	3.09×10^{10}	20	0.08	4.0

which hatched around the second week in October, appeared to move rapidly southwestward.

Assuming that these patches originated from one of the documented spawning sites, there is a seasonal difference in the pattern of their dispersal. The larvae that hatched earlier appear to have been retained near the spawning site longer, while those that hatched later seemed to have moved more rapidly away from the spawning sites.

Mortality was calculated from the change in size of cohorts (C1-C3-C5 and B1 + B2 − 3) observed in successive cruises. Patch size was estimated as the sum (for all stations containing that patch) of the density of a particular size group (No.·m^{-3}) × station depth (m) × station area (m^{-2}).

Mortality (Table 3) is expressed as both the instantaneous rate (Z);

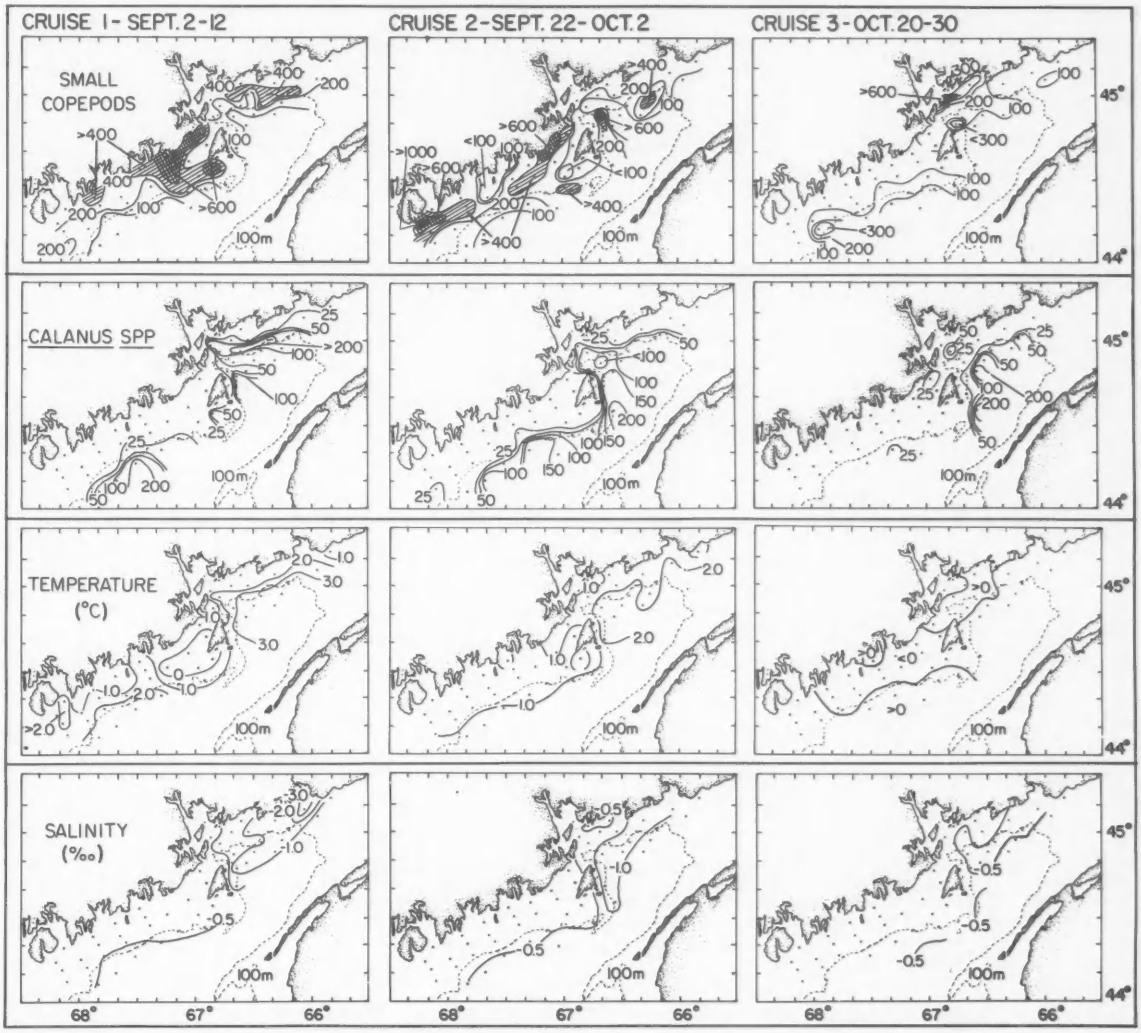

FIG. 5. Spatial distribution of small copepods and *Calanus* sp. (No.·10 m^{-3}), and of vertical differences (surface − bottom) in temperature and salinity during three surveys of coastal waters of eastern Maine and southwestern New Brunswick; September and October 1986.

$$\frac{Nt}{No} = e^{-Zt}$$

and as a simple percentage of the original cohort size;

$$\frac{\frac{(No - Nt)}{t}}{No} \times 100,$$

where *No* is the initial cohort size and *Nt* is the cohort size at time *t*. Instantaneous mortality rates ranged from 0.05–0.08·d^{-1}; percentage mortality was between 3 and 4%·d^{-1}.

This mortality rate is similar to that reported by Lough et al. (1980; 4% for the first 100 d on Georges Bank) and Heath and MacLachlan (1987; 2% over first 7 d), but lower than the estimates of Munk et al. (1986; 10% for older larvae in general) and Graham and Chenoweth (1973; 30% for newly hatched larvae on Georges Bank).

Corresponding Oceanographic Features

The outstanding oceanographic feature which seemed to relate to the location of herring spawning sites and to the area of larval dispersal west of Grand Manan was a sharp discontinuity that encompassed the spawning grounds except southwest along the coastal shelf (Fig. 5). On each side of this line, the temperature and salinity structure of the water column were different as was the species composition of pelagic copepods. Our hydrographic observations support previous studies which noted that vertically homogeneous waters around the southern entrance to the Grand Manan channel contrasted with more stratified water offshore (Hachey 1952) and that there are "…strong and persistent summertime fronts near the mouth of the Bay of Fundy, along part of the Maine coast…" (Loder and Greenberg 1986). We too interpret this discontinuity to be an ocean front which extended from the northern entrance to the

Grand Manan channel, along the coastal shelf at the 100-m isobath to at least Mt. Desert Island. The front separated vertically homogeneous water inshore from more stratified water offshore. This discontinuity displayed by the hydrographic and zooplankton data was very distinct during the first two cruises but was less so on the third cruise, indicating that the front was breaking down by late October. There was a striking correspondence between the distribution of herring larvae (Fig. 2) and these oceanographic features (Fig. 5), particularly during the first cruise.

Thermal stratification in the water column, as indicated by the difference between surface and bottom temperature (Fig. 5), was evident offshore along the 100-m isobath during the first two cruises, with a tongue extending towards the entrance to Passamaquoddy Bay across the northern entrance to Grand Manan Channel. More vertically homogeneous waters were found along the coastal shelf between the entrance to Grand Manan Channel and Mt. Desert Island, particularly near the spawning grounds during the first cruise. By late October there was little evidence of significant stratification anywhere in the study area.

Vertical differences in salinity showed a similar pattern to that of temperature. Southwest of Grand Manan, there was no stratification inside the 100-m isobath. The obvious feature was the plume of low salinity water that moved out of the Saint John River and influenced surface salinity across the entrance of Passamaquoddy Bay and around the eastern side of Grand Manan. The outflow from the Saint John River has been identified by Huntsman (1953) as influential in the movement of water out of the Bay of Fundy and around the eastern side of Grand Manan. By the third cruise the Saint John plume had diminished considerably and there was less intense stratification.

The species composition of planktonic copepods showed two distinct faunas. The oceanic community consisted primarily of *Calanus finmarchicus* (Fig. 5), but also included *C. hyperboreus*, and *Euchaeta* sp. The inshore limit for the dominance of this community ran along the 100-m isobath with a distinct tongue towards the entrance to Passamaquoddy Bay. The neritic community was dominated by the small copepods *Temora* sp., *Pseudocalanus* sp., and *Centropages* sp. The most dense aggregation during the first cruise was found along the eastern Maine shore to about Machias Bay and just southwest of Grand Manan, while a lesser aggregation was found between Passamaquoddy Bay and Saint John. By the second cruise, there was evidence that the major aggregation in Grand Manan Channel had extended to the west towards another high density area off Mt. Desert, while small patches of neritic copepods appeared to move around the eastern shore of Grand Manan in a manner suggesting, as did the salinity data, a movement of water out of the Saint John area and around the eastern side of Grand Manan. On the third cruise dense concentrations of *Calanus finmarchicus* were limited to the deeper water of the Bay of Fundy, while only small, isolated patches of neritic copepods remained along the central shelf.

Discussion

Origin of Larvae East and West of Grand Manan

The striking discontinuity in distribution and the dissimilar size frequency of larval herring east and west of Grand Manan suggests that the larvae in each area were of different origin.

The larvae east of Grand Manan were large (>12 mm), relatively few in number, and concentrated at the eastern end of the survey area off Saint John. Most were more than a month old; the area contained no newly hatched larvae. This group represents the edge of a large patch of larvae that was observed and sampled in 1986 off Digby, Nova Scotia (R. Stephenson, unpubl. data) and in previous annual Bay of Fundy surveys (Iles et al. 1985) and probably originated off southwest Nova Scotia or the eastern Bay of Fundy.

The larvae west of Grand Manan clearly originated from spawning beds in the shoals southwest of Grand Manan and in Maine's coastal waters off Machias Bay and Cutler Harbor. The location of the herring spawning ground that we have inferred from the distribution of early larvae (Fig. 1) is consistent with earlier reports based on larval distribution (Townsend et al. 1986), egg deposition locations (Stevenson 1984), and location of spawning adults (Moore 1898; Huntsman 1953; Bigelow and Schroeder 1953). Our data suggest an extended period of hatching in 1986 from late July to mid-October. This initial hatch is somewhat earlier than that of late August reported by Graham et al. (1984).

The abrupt eastern margin that was characteristic of the coastal Maine larval aggregation persisted for the 2 mo of our survey. This same eastern discontinuity has been shown to occur annually and to persist until November in larger scale surveys (Iles et al. 1985). There does not appear to be immigration of herring larvae into eastern Maine waters from spawning in the Bay of Fundy and southwest Nova Scotia, which supports the view of Graham et al. (1984) that herring larvae in coastal Maine waters result from local spawning. The eastern Maine–Grand Manan spawning group appears to be an autonomous, recurring spawning unit with its own separate larval distribution.

Dispersal of Larvae West of Grand Manan

The distribution of larval herring west of Grand Manan coincided, at least for the first two cruises, with a coastal area of well mixed water (Fig. 5) lying within the 100-m depth contour. This water mass was characterized by high densities of small, neritic copepods and was very different in its faunal content from the offshore, more stratified water dominated by the oceanic copepod, *Calanus finmarchicus*. The occurrence of larval herring within well mixed, shallow waters is a pattern which has been observed in other areas (Iles and Sinclair 1982). By the third cruise, the frontal boundary appeared to have broken down, but the larvae were still found within the 100-m contour.

Opposing hypotheses relevant to the dispersal of herring larvae in this area have been put forward. Previous studies in coastal Maine waters (Graham 1982; Graham et al. 1984; Graham and Townsend 1985; Townsend et al. 1986) concluded that larvae which hatch in eastern Maine drift westward before eventually entering coastal bays and estuaries. Iles and Sinclair (1982), on the other hand, predicted that larvae should be retained within well mixed larval retention areas in the vicinity of spawning.

The temporal pattern of larval distribution over the three cruises (Fig. 4) shows instances where patches remained in the general area of hatching (for example patches C1-C3-C5)), but others where there was displacement of larvae to the west (patches C4 and D). The pattern of dispersal appears to have changed over the survey period. For instance, the distribution of the 7–12 mm (approximately 3-wk-old) larvae in successive cruises shows a change from what was initially larval persistence near the spawning ground during the first cruise, to a significant and rapid displacement of larvae to the westward in the

third cruise (Fig. 4). This may be related to an apparent change in oceanographic conditions, exemplified by the breakdown of stratification along the 100-m contour which occurred between the second and third cruises.

There may also be aggregation or accumulation of larvae in the area southwest of Jonesport; in only one case (13+ mm larvae in the third cruise) was there evidence of the movement of a larval patch beyond the western margin of the study area. The occurrence of two areas of high concentration, one just west of Grand Manan and the other southwest of Jonesport (Fig. 2) seems to be a persistent pattern. It is obvious in each of our surveys and also in previous data (Townsend et al. 1986; Graham 1982) and may reflect hydrographic features such as eddies or some behavioral characteristic of the larvae.

Hydrographic studies have shown that the survey area is one of extreme tidal mixing and one in which the residual currents do not appear to demonstrate a continuous, dominant flow in any direction. The major current flowing out of the Bay of Fundy moves along the western shore from Saint John to the mouth of Passamaquoddy Bay, around the eastern shore of Grand Manan and then southwestward along the Maine coast (Bigelow 1927; Fish and Johnson 1937; Hachey 1952; Huntsman 1953). The shoreward boundary of this current may be associated with the line of discontinuity we observed in our data (Fig. 5). Inshore of this, from about Petit Manan to the northern entrance of Grand Manan Channel, the waters are virtually homogeneous top to bottom. Observations of residual drift have been made in this area using information from drift bottles, current measurements and other hydrographic parameters, but with conflicting results. The area has been described as a region of "dead water" (Fish and Johnson 1937; Hachey 1952), containing a small eddy running inward on the Grand Manan shore and outward along the Maine coast (Bigelow 1927), or containing a series of complex eddies (Greenberg 1983). The dominant flow of residual currents through the channel and along the Maine coast has been described as moving northward (Watson 1936) or southward (MacGregor and McLellan 1952; Townsend et al. 1986). What dominant residual flow there is near Grand Manan channel may be variable, at times not moving appreciably and at times moving parallel to the coast.

Dispersal from the spawning ground seems more complex than a simple stream of larvae drifting westward into waters where a greater density of food organisms occurs (Townsend et al. 1986) or the complete retention of larvae near the spawning site. Our results indicate changing patterns of larval dispersal ranging from persistence within the general vicinity of spawning to rapid westward movement. Larvae appear to remain aggregated during this period and do not spread out like a plume from a point source. These complexities of larval distribution argue for a more selective movement of individual aggregations.

Independent movement of individual aggregations would not be surprising in light of what appears to be variability in the residual currents near the spawning ground and vertical mobility of the larvae. Larval herring are not completely passive in the water column. Studies off southwest Nova Scotia (Stephenson and Power 1988) and in the Gulf of St. Lawrence (Fortier and Leggett 1983) have shown definite vertical movement of herring larvae, raising the possibility of an active behavioral component to larval dispersal.

Acknowledgements

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Migration Timing, Size, and Salinity Tolerance of Sea-Type Sockeye Salmon (*Oncorhynchus nerka*) in an Alaska Estuary

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Migration timing, size, and salinity tolerance were determined for sea-type sockeye salmon (*Oncorhynchus nerka*), which migrate to sea as underyearlings (age-0), in the Situk River estuary, Southeast Alaska. Ten sites in three habitat types were seined monthly from late April through August, 1987, and age-0 sockeye from the estuary were tested for salinity tolerance. Age-0 sockeye were most abundant (up to $13 \cdot m^{-2}$) from late April through June, and by late July, most sockeye had left the estuary. Mean fork length (*FL*) was 31 mm in April and increased 0.4 $mm \cdot d^{-1}$ to 70 mm in late July when most (72%) remaining sockeye had grown to about the same size as age-1 smolts (69–95 mm) emigrating in May and June. Mean *FL* of age-0 sockeye in the estuary in July was 23 mm greater than in freshwater areas of the river. Salinity tolerance was directly related to fish size, and a size of at least 50 mm was required for 100% survival in seawater. Because salinity in the estuary ranged 0–30‰, sockeye of all sizes could survive in the estuary. Thus, in 3–4 mo, sea-type sockeye attained a size large enough to adapt to seawater and migrate to sea.

Le moment où s'effectue la migration, la taille et la tolérance à la salinité ont été déterminés pour le saumon rouge de mer (*Oncorhynchus nerka*) dont les alevins de moins d'un an vont vers la mer dans l'estuaire de la rivière Situk dans le sud-est de l'Alaska. Entre la fin d'avril et la fin d'août 1987, les saumons de moins d'un an ont été prélevés mensuellement dans l'estuaire au moyen de senneurs à dix sites répartis dans trois types d'habitat; leur tolérance à la salinité a ensuite été évaluée. Les saumons de moins d'un an étaient les plus abondants (densité atteignant $13 \cdot m^{-4}$) de la fin d'avril à la fin de juin; à la fin de juillet, la plupart des saumons avaient quitté l'estuaire. La longueur moyenne à la fourche était de 31 mm en avril; elle a augmenté de 0,4 $mm \cdot^{-1}$ pour atteindre 70 mm à la fin de juillet, alors que la plupart des saumons rouges qui restaient (72 %) avaient atteint à peu près la taille des smolts d'un an (69–95 mm) qui émigrent en mai et en juin. La longueur à la fourche moyenne des saumons rouges de moins d'un an présents dans l'estuaire en juillet était de 23 mm supérieure à ceux qui se trouvaient dans les zones d'eau douce de la rivière. Les auteurs ont observé que la tolérance à la salinité était directement proportionnelle à la taille du poisson et qu'un saumon rouge devait atteindre au moins 50 mm pour que sa survie soit de 100 % dans l'eau de mer. Puisque la salinité dans l'estuaire variait entre 0–30 ‰, des saumons rouges de toutes les tailles pouvaient y survivre. Ainsi, en 3–4 mo, les saumons rouges de mer atteignaient une taille suffisamment grande pour leur permettre de s'adapter à l'eau salée et de migrer vers la mer.

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Sockeye salmon (*Oncorhynchus nerka*) typically rear in freshwater lakes for one or more years before migrating to sea as smolts. Scale analysis has identified a different life-history type (Foerster 1968; Bugaev 1987; Wood et al. 1987); sea-type sockeye which migrate to sea at age-0, without spending a winter in fresh water. Although sea-type sockeye were originally identified in the early 1900's by Gilbert (1918), only recently have managers recognized their importance to some fisheries. Sea-type sockeye usually make up only a small proportion of catch from a river system (Foerster 1968), but they comprise nearly all the catch in some Alaska fisheries (Pahlke and Riffe 1988).

Information on the early marine life of sea-type sockeye is scarce. The only published information is from the Fraser River estuary in British Columbia (Healey 1980; Birtwell et al. 1987), which indicates that sea-type sockeye rear in the estuary a few months before going to sea. In this paper, we document the rearing of age-0 sockeye salmon in saline waters of the Situk River estuary near Yakutat, Alaska, where up to 20% of the sockeye catch is sea-type (Pahlke and Riffe 1988). The objectives of this study were to determine the migration timing and salinity tolerance of age-0 sockeye salmon in the Situk River estuary and to compare size of age-0 sockeye from estuarine and freshwater areas.

Methods

This study was conducted in the estuary of the Situk River, 13 km south of Yakutat, Southeast Alaska (Fig. 1). In addition to the Situk River, other salmon-producing streams flow into the estuary, including Kunayosh Creek, Seal Creek, and the glacial Ahrnklin River. Thus, fish captured in the estuary may have originated from streams other than the Situk River. Riffe (1987) provides a detailed description of the Situk River watershed and commercial fisheries.

Sampling was restricted to a 12-km^2 area near the mouth of the Situk River. The estuary in this area consisted of three distinct habitats: (1) a 1.3-km reach of the lower Situk River chan-

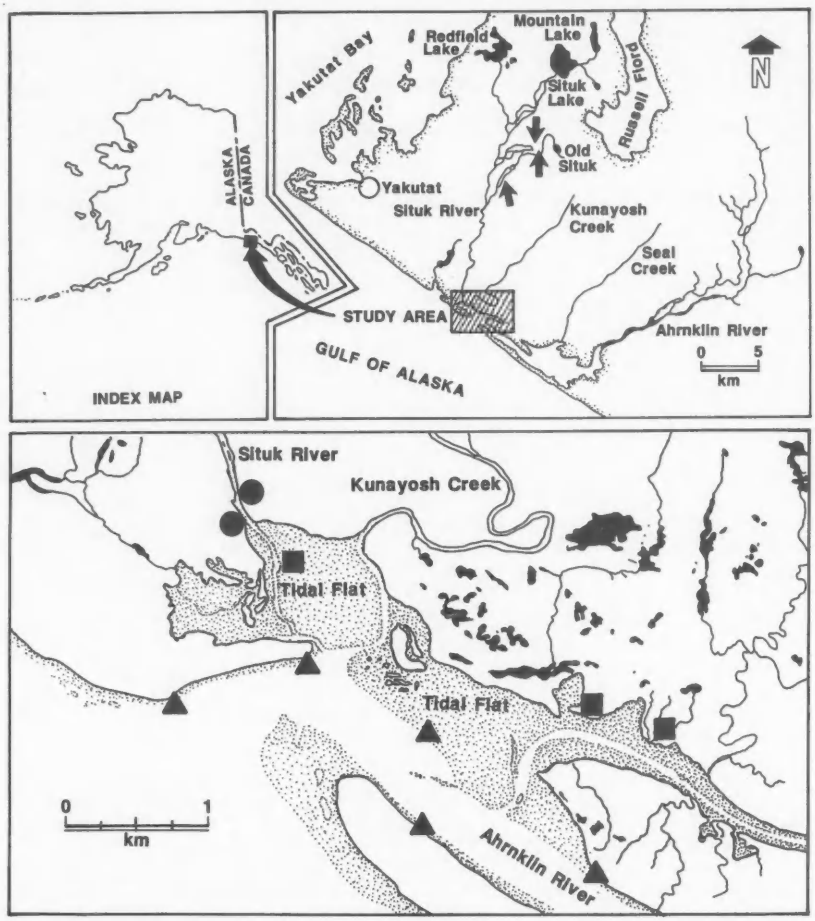

FIG. 1. Location of the sampling stations in the basin (triangles), river channel (circles), and tidal sloughs (squares) in the Situk River estuary, Alaska. Three sites sampled in freshwater areas of the Situk River are shown as arrows.

TABLE 1. Mean physical characteristics (range in parentheses) of sampling stations in three habitat types in the Situk River estuary, Alaska, late April through August 1987.

Characteristic	River channel	Basin	Tidal slough
Surface salinity (‰)	0.5 (0.0–1.5)	16.7 (0.0–28.9)	14.5 (1.0–21.0)
Bottom salinity (‰)	4.3 (0.0–29.0)	20.5 (0.0–30.0)	14.7 (3.4–21.3)
Water temperature (°C)	8.9 (3.8–12.7)	10.2 (5.6–15.0)	11.0 (4.0–15.1)
Depth (m)	0.4 (0.1–1.4)	4.1 (0.5–7.9)	0.3 (0.1–0.5)

nel which was periodically inundated by tides; (2) a 6-km^2 basin; and (3) numerous small (1–6 m wide) tidal sloughs lined with *Carex* sp. A surface lens of low salinity (0–1‰) was present at all habitat types (Table 1), particularly in the river channel and tidal sloughs which had proportionately more freshwater input than the basin. Although salinity varied by tide, salinity generally was lower in the river channel and tidal sloughs than in the basin. Water temperature ranged from 3.8°C in April to a high of 15.1°C in late July. Water depth at low tide averaged 0.4 m in the river channel, 4.1 m in the basin, and 0.3 m in the tidal sloughs.

Ten sampling stations were established: two in the river channel, five in the basin, and three in tidal sloughs (Fig. 1). Stations usually were seined once each month from 20 April to 25 August 1987. At each station in the river channel and basin, three separate areas, 20–50 m apart, were sampled with a seine 28 m long and 3 m deep, with 13-mm stretch mesh on the wings, and a central bag of 6-mm stretch mesh. The seine was set parallel to and 35 m from shore by skiff, and retrieved from shore. Catch per unit effort (CPUE) for each station was computed as the mean catch at the three separate areas. CPUE's could not be compared between stations because the capture efficiency of the beach seine was not determined at each station. In tidal sloughs, a 50-m reach was blocked at the upper and lower ends with seines (6-mm mesh), and a small pole seine (2.7 m long, 6-mm mesh) was used to capture fish. Number of sockeye was estimated by the removal method with at least three

TABLE 2. Mean catch per unit effort (river channel and basin) and mean density (No.·m^{-2}; tidal slough) of age-0 sockeye by sampling period and habitat type, Situk River estuary, Alaska 1987. Number of sites sampled (n) and ranges are shown in parentheses.

Habitat type	April (n=6)	May (n=8)	June (n=10)	July (n=8)	August (n=8)
River channel	4.1 (1.7–6.6)	10.8 (6.9–16.7)	12.7 (2.9–22.5)	2.0 (0.0–2.9)	0.3 (0.0–1.0)
Basin	11.2 (4.0–20.3)	0.3 (0.0–1.0)	23.5 (0.7–65.6)	0.4 (0.0–1.3)	0.0 (0.0–0.0)
Tidal slough	[a]	12.8 [b]	0.4 (0.0–1.0)	<0.1 (0.0–0.1)	<0.1 (0.0–<0.1)

[a]Tidal sloughs were not sampled in April.
[b]Only one tidal slough was sampled in May.

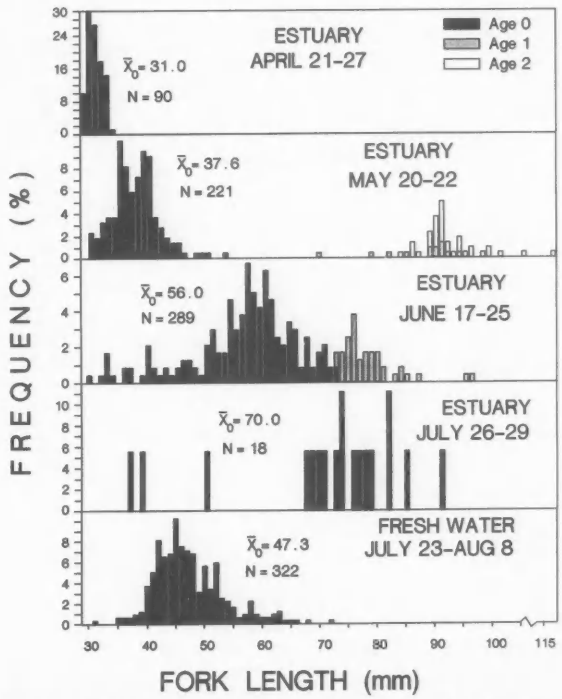

FIG. 2. Length frequencies of sockeye salmon from the Situk River estuary, Alaska, from late April through July and from freshwater areas of the Situk River in July–August, 1987. Mean length of age-0 sockeye ($\bar{X}_0$) and total number of sockeye measured (N) are shown for each sampling period.

passes (Zippin 1958), and density was calculated by dividing the estimated number by the reach area.

All fish captured were identified and counted, and a random sample was measured for fork length (FL). To compare size of age-0 sockeye in the estuary with those in fresh water upriver, we measured a random sample of sockeye from the Old Situk River and two unnamed tributaries (Fig. 1) in late July and early August. To separate age-0 sockeye from older sockeye, scale samples were taken from a range of sizes in the catch.

Salinity tolerance bioassays were used to determine the ability of age-0 sockeye to survive in seawater. In May and June, fish were collected from tidal sloughs and placed in 60-L plastic containers filled with aerated water at 0, 26, 28, or 30‰ salinity at ambient temperature (mean 10.0°C in May and 9.1°C in June). Ocean water was mixed with either fresh water or Instant Ocean[1] salts to obtain desired salinity. To avoid overcrowding, no more than 15 fish were placed in each container. Mortalities were removed and measured every 12 h.

TABLE 3. Comparison of percent survival in May and June of three size groups of age-0 sockeye salmon from the Situk River estuary, Alaska, after 96 h in 26–30‰ salinity. Significance (P) was based on Fisher's exact test. Sample size is shown in parentheses.

Fork length (mm)	Percent survival		P
	May	June	
30–39	53.3 (15)	60.0 (10)	0.53
40–49	71.4 (14)	78.9 (19)	0.82
50–59	(0)	100.0 (15)	

Results

Age-0 sockeye migrated through the estuary from April to late July. Age-0 sockeye salmon were already present in the estuary at the start of sampling in late April; abundance peaked in May–June; and most had left the estuary by late July (Table 2). Age-1 and -2 sockeye were present only in May and June. In the river channel, CPUE of age-0 sockeye peaked in May and June, when large schools occupied channel margins, and declined to nearly zero by late July. In the basin, CPUE was more variable: high in April when many age-0 sockeye were in the ocean surf at the basin mouth, nearly zero in May, highest in June, and nearly zero thereafter. In tidal sloughs, density was highest in May when sampling began and declined sharply thereafter.

Size of age-0 sockeye in the estuary increased rapidly. In late April, mean FL of age-0 sockeye was 31 mm (Fig. 2), about the same size as newly emergent fry. By late July, mean FL was 70 mm (an increase of 0.4 mm·d^{-1} from late April) and 72% of the age-0 sockeye were about the same size as age-1 smolts (range, 69–95 mm) caught in May and June. Even though mean FL increased rapidly, small (<40 mm) sockeye were always present. In July, size ranged widely; 37–90 mm FL. Whether the smaller fish emerged and migrated to the estuary late or grew slowly while in the estuary was not determined. Age-0 sockeye from freshwater areas of the Situk River were significantly (P <0.05, F test) smaller than those from the estuary (Fig. 2). Age-0 sockeye in fresh water in late July and

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

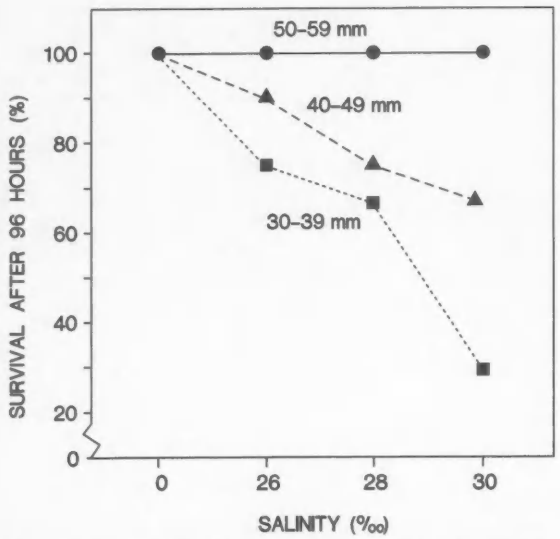

FIG. 3. Percent survival of three size groups of age-0 sockeye salmon from the Situk River estuary, Alaska, after 96 h in 0, 26, 28, and 30‰ salinity.

early August averaged 10 mm smaller than in the estuary in late June, and 23 mm smaller than in the estuary in late July.

In the salinity tolerance tests, survival of age-0 sockeye was directly related to fish size. Survival was substantially better in June than in May; 82% survived in 26–30‰ salinity in June compared with only 62% in May. Higher survival in June was mostly because of larger fish size; 50–59 mm sockeye, which had 100% survival, were present in June but absent in May. Although survival of fish of similar length tended to be greater in June than in May, differences were not significant ($P > 0.5$; Table 3). For combined May and June data, survival was inversely related to salinity and strongly dependent on fish length ($P < 0.02$; Chi-square test; Fig. 3). Survival in 30‰ was 30% for 30- to 39-mm, 67% for 40- to 49-mm, and 100% for 50- to 59-mm sockeye. About two-thirds of the mortalities occurred within 24 h, and all fish in fresh water survived. Thus, differences in survival between May and June were caused by differences in fish size, and a size of at least 50 mm was required for 100% survival in seawater.

Discussion

Age-0 sockeye were present in the estuary from late April to late July, a period of about 3 mo. While this period represents "species" residence time, it does not represent "individual" residence time (Simenstad et al. 1982). Age-0 sockeye may migrate from the river to the estuary and from the estuary to the ocean at various times. In the Stikine and Taku Rivers in British Columbia and Alaska, age-0 sockeye migrate downstream toward the estuary from late April until early November (Heifetz et al. 1987; Wood et al. 1987; M. L. Murphy, Auke Bay Laboratory, P.O. Box 210155, Auke Bay, AK 99821, unpubl. data). Thus, sea-type sockeye may have a number of life-history patterns that differ in duration of residence in fresh water and the estuary, similar to the variety of life histories described for chinook salmon (*O. tshawytscha*) (Levy 1984; Neilson et al. 1985).

Salinity in the estuary ranged widely (0–30‰) and, therefore, may have influenced distribution of age-0 sockeye, especially in April and May when most fish were smaller than 50 mm. The basin often had higher salinity (30‰) than sockeye <50 mm could tolerate, based on salinity tolerance tests. Thus, newly emerged fish that were common in the basin in April probably either perished or moved to areas with lower salinity, such as the river channel or tidal sloughs. Some may have been involuntarily washed out to sea, as indicated by the age-0 sockeye observed in ocean surf near the mouth of the basin in April. While abundance declined in the basin between April and May, it increased in the river channel. In late June, age–sockeye were again common in the basin. By this time, most sockeye were larger than 50 mm and presumably could survive at sea. Birtwell et al. (1987) concluded that salinity did not influence distribution of age-0 sockeye in a section of the Fraser River estuary. Salinities reported by Birtwell et al. (1987), however, were much lower (0.1–8.1‰) than in our study.

Size of age-0 sockeye increased rapidly in the estuary. By late July, age-0 sockeye in the estuary were about the same size as age-1 smolts and were larger than age-0 fish from freshwater areas of the river, even though the largest of the age-0 sockeye probably had already migrated to sea. Thus, in less than 3 mo, age-0 sockeye in the estuary had equaled a year's growth in fresh water. Similar rapid increases in size ("apparent growth rate") were reported for age-0 sockeye in the Fraser River estuary (Healey 1980; Birtwell et al. 1987). This suggests that growth in the estuary was better than in fresh water. The rapid increase in size, however, may not be attributable solely to estuarine growth because emergence time and time of arrival to the estuary of individual cohorts were not known.

We hypothesize that estuarine rearing enables sockeye to grow large enough to adapt to seawater and migrate to sea as underyearlings. To test this hypothesis, future research should compare growth and habitat use of age-0 sockeye in fresh water and estuarine rearing areas in relation to emergence and migration timing, water temperature, and prey availability.

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Biologically Available Phosphorus: Estimation and Prediction Using an Anion-Exchange Resin

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The suitability of ion-exchange resin extraction for assessing biologically available P (phosphorus) concentrations was evaluated in a wide range of water samples of different origins (natural waters, wastewater treatment plant effluents, and industrial effluents). A recycling system was specifically designed to enhance P adsorption by the resin by maintaining a steep P gradient. Resin extractable P compared favorably with total P, total soluble P, and soluble reactive P, as a predictor of bioassay available P (BAP). Biologically available P was generally greater than soluble reactive P and less than total soluble P. Over the diverse water samples tested, the best model for predicting BAP used resin extractable P and soluble reactive P.

L'extraction sur résine échangeuse d'ions a été évaluée comme méthode d'estimation de la concentration de P (phosphore) biodisponible dans une vaste gamme d'échantillons d'eaux d'origines diverses (eaux naturelles, effluents d'épuration d'eaux usées et effluents industriels). Un système de recirculation a été spécialement conçu pour favoriser l'adsorption de P sur la résine en maintenant un gradient élevé de P. Le P extrait par la résine se compare favorablement au P total, au P total dissous et au P réactif soluble comme mesure du P biodisponible. La concentration de ce dernier est généralement supérieure à celle du P réactif soluble et inférieure à celle du P total dissous. Compte tenu des différents échantillons d'eaux testés, la meilleure estimation du P biodisponible est donné par le modèle qui utilise à la fois le P adsorbé sur résine et le P réactif soluble.

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Contemporary programs for eutrophication abatement seek to control all forms of P (phosphorus) irrespective of whether the P is in a form which could support algal growth (Lee et al. 1980). Nevertheless, there is ample evidence (Golterman 1976; Peters 1981; Sonzogni et al. 1982) that bioavailability varies among P forms and that some of the P entering lakes has a very limited effect on lake productivity and eutrophication. Abatement programs directed towards reduction of bioavailable P might be more effective than total P control but development of the former depends on the identification of a precise, cost-effective analytical estimator of bioavailable P.

Two approaches for assessing biologically available P have received special attention. The first technique is a bioassay derived from the Algal Assay Procedure developed by the US-EPA (1971); although it represents the most direct measure of bioavailable P, it is tedious and time-consuming. The second technique, based on sequential chemical extraction, was originally developed by soil scientists, and adapted to characterize P in lake sediments (Williams et al. 1971). Although significant correlations have been found between bioavailable P and NaOH extractable P, the correlation coefficients are much lower than those between bioavailable P and total P, and the aggressive reagents used in the extraction may release phosphorus which is not normally available (Klapwijk et al. 1982). This release is especially problematic when diverse water sources, with diverse P forms, are to be compared. Since neither of these techniques is appropriate for routine use, a quicker, but still accurate, measure of P bioavailability is needed.

Several other analytical estimators of biologically available P have been suggested. Significant correlations have been found between P bioavailability in lake sediments and total P (Klapwijk et al. 1982), organic P, and inorganic P (Grobbler and Davies 1979). Other studies estimate P bioavailability of lake waters as total soluble P (Schaffner and Oglesby 1978; Broberg 1983; Bradford and Peters 1987) or soluble reactive P (Walton and Lee 1972; Chamberlain and Shapiro 1973; Nürnberg and Peters 1984). However, neither soluble P, particulate P, soluble reactive P, orthophosphate, large molecular weight P (>5000 molecular weight) nor small molecular weight P (<400 molecular weight) describe trophic response better than did total P, in natural waters (Peters and Bergmann 1982).

Under the premise that bioassay P effectively measures bioavailable P, any chemical procedure to estimate P bioavailability must correlate well with bioassay estimates. The technique should also be applicable to a wide range of samples, it must be relatively easy to perform, it must yield reproducible results, and it must not alter the chemical forms of P in the sample. Phosphate extractions from soils by anion-exchange resin (Amer et al. 1955; Moser et al. 1959; Cooke and Hislop 1963) suggest that this technique may meet these criteria. Anion-exchange resins should minimize chemical degradation, for they absorb phosphate without affecting other chemical characteristics of the sample (Amer et al. 1955; Cooke and Hislop 1963). Theoretically, resin extraction should assess P bioavailability

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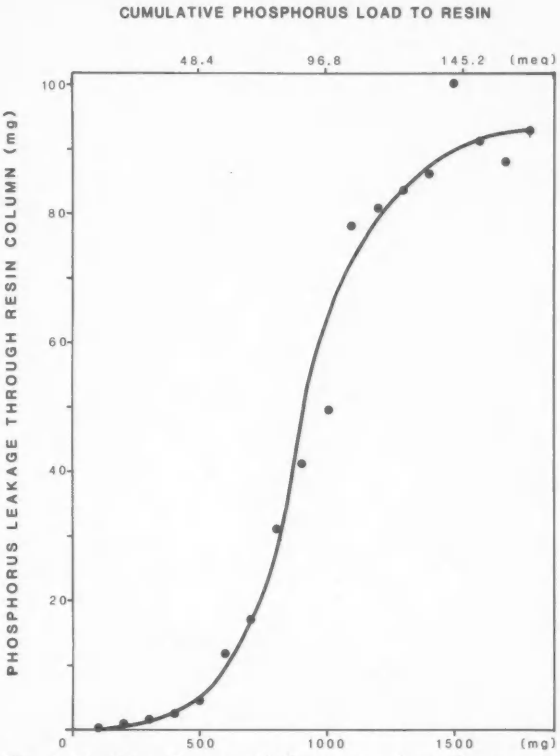

FIG. 1. Breakthrough curve of the strong anion-exchange resin: DUOLITE A 101D.

since it measures the inorganic P that mediates exchange reactions between the solid and dissolved P phases (Sonzogni et al. 1982). The anion-exchange resin acts as a "sink" that displaces the equilibrium between particulate and dissolved P in the direction of the aqueous phase. The presence of the resin "sink" therefore increases the quantity of phosphorus released to solution, until most exchangeable P is ultimately adsorbed by the resin. Huettl et al. (1979) found a highly significant correlation between bioassay available P and P sorbed by resin-affixed hydroxy–aluminum equilibrating with five simulated sediment suspensions. However, P equilibrations with an anion-exchange resin mixed directly with sediment suspensions underestimated the total amount of bioavailable P (Cowen and Lee 1976; Armstrong et al. 1979).

This study was undertaken to determine the relationships between the amount of P that algal assay shows to be available (BAP), the amount of P extracted from a water sample by an anion-exchange resin, and some of the more commonly analyzed P fractions. Unlike previous studies which were limited to few samples of lake sediments and urban runoff, this study involved a wide range of samples of different origins. The results allow an evaluation of the utility of an anion-exchange resin for quantifying P bioavailability in surface waters.

Materials and Methods

Resin Extraction

A strongly basic anion-exchange resin (DUOLITE A 101D, 13,33–53,33 mesh) was used as the P-adsorbing matrix. After

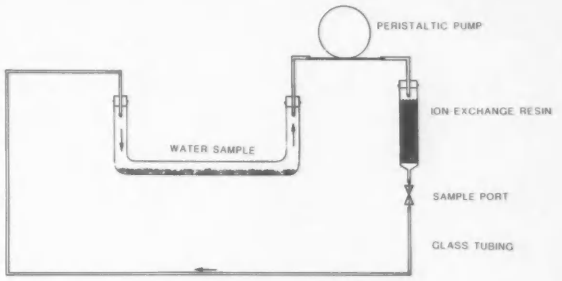

FIG. 2. Experimental apparatus.

swelling, 50 mL of resin were loaded into an ion-exchange column (4-cm diameter). The ion-exchanger was converted from the chloride form to the hydroxide form by flushing the resin with 0.1N (0.1 eq·L^{-1}) NaOH at a flow rate of 16 mL·min^{-1}. The resin was then washed with distilled water until the pH of the elutriate reached 6.

The effective capacity of this resin, defined as the total quantity of counterions fully utilized in an exchange column, was determined by 18 successive percolations of 1-L solutions of 100 mg·L^{-1} (9.68 meq·L^{-1}) of P added as K_2HPO_4. After each percolation, the leachate was analyzed for total P, to measure "P leaks", the proportion of PO_4 which was not adsorbed by the resin (Fig. 1). The effective capacity of the 50 mL of swollen resin, estimated by subtracting the sum of all P leaks (83.5 meq or 862.1 mg P, area under the "breakthrough curve"; Fig. 1) from the sum of all P inputs (174 meq or 1800 mg P), was determined to be 91 meq of anions.

Phosphorus leakage increases gradually with increasing cumulative P load to resin, indicating decreasing resin efficiency (Fig. 1). After the addition of 500 mg P (48.4 meq P), the cumulative leakage of P is only 10.8 mg P, indicating that the 50 mL of resin extract 48.4 meq of anions with 98% efficiency. Saturation of the exchange sites by extraneous anions (water-soluble salts) can be avoided by diluting the water samples to insure that the total quantity of anions does not exceed 48.4 meq.

Previously extractions were carried out with resin directly mixed with the suspended sediments (Cowen and Lee 1976; Armstrong et al. 1979; Huettl et al. 1979). This study employed a recycling system (Fig. 2) in which the sample was separated from the resin, thereby maintaining a steep P gradient between the particulate matter and the water to maximize leaching of P from the particulate fraction.

To extract phosphorus, 500 mL of sample were continuously cycled through the ion-exchange bed at a flow rate of 16 mL·min^{-1} for 24 h. Following this extraction, the resin was thoroughly washed with 4 L of distilled water to remove unadsorbed P. The exchanged anions were then recovered by leaching with 500 mL of 1N Na_2SO_4 (1 eq·L^{-1}). Total P in the leachate was analyzed to yield the amount of exchangeable P in the sample. The accuracy of this resin extraction technique (estimated as the coefficient of variation, CV, of four extractions of standard P solutions of 25 to 100 mg·L^{-1} P) is 1.01% and its precision (estimated as the CV of three replicate extractions) is 0.86%.

Bioassays

The bioassays were carried out using the "batch" technique and an alternative of the "Bottle Test" developed by Steeman-

TABLE 1. Summary of the descriptive statistics of the data set (n = 50, BAP = bioassay available P, REP = resin extractable P, SRP = soluble reactive P, TSP = total soluble P, TP = total P).

	Range ($\mu g \cdot L^{-1}$)	Mean ($\mu g \cdot L^{-1}$)	Median ($\mu g \cdot L^{-1}$)	%TP	%BAP
BAP	$0–1.984 \times 10^5$	1.506×10^4	3.340×10^3	58	100
REP	$18–1.535 \times 10^5$	9.701×10^3	3.880×10^3	54	92
SRP	$0–3.310 \times 10^4$	4.129×10^3	2.680×10^3	23	39
TSP	$4–2.501 \times 10^5$	1.227×10^4	4.045×10^3	68	116
TP	$21–2.722 \times 10^5$	1.809×10^4	6.030×10^3	100	171

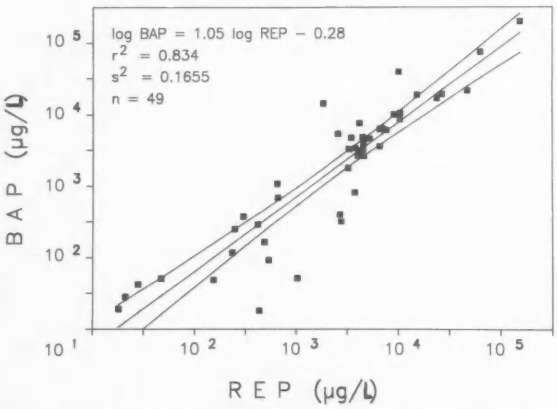

FIG. 3. Relationship between resin extractable P (REP) and bioassay available P (BAP).

Nielsen and Hansen (1961). The samples were enclosed in dialysis tubing to eliminate interference by indigenous algae while minimizing the alteration of bioavailability caused by filtration or autoclaving (Hanna 1985). A dialysis bag containing 50 mL of water was dropped into an Erlenmeyer flask containing culture media inoculated with *Scenedesmus crassus*. The dialysis tubing (VISKING regenerated cellulose, average pore diameter = 2.4 nm) is permeable to water and to solutes <12 000 molecular weight. The cultures were incubated at 20°C with a light intensity of 70 µE for a light:dark cycle of 15:9 for 3 wk. Since all nutrients, except P, were present in excess, cessation of growth was taken to indicate P limitation. In this system, P bioavailability was estimated by algal yield (Hanna 1985), measured as the final optical densities of the cultures at 678 nm (Cloern 1976). This bioassay technique has an accuracy of 4% (CV of analyses of 20 P standards) and a precision of 3.95% (CV of three replicate samples).

Chemical Analysis

Phosphorus concentrations were determined with the molybdenum blue technique using ascorbic acid (Stephens 1963). Analyses of total phosphorus (TP) and total soluble phosphorus (TSP) followed potassium persulfate digestion (Gales et al. 1966). Particulate P was removed by filtration through 0.45-µm Millipore filters, and the filtrate analyzed for soluble reactive P (SRP) or, after digestion, for TSP.

Water Samples

Tests were carried out on 50 water samples which can be grouped into four major classes: nine natural waters sampled

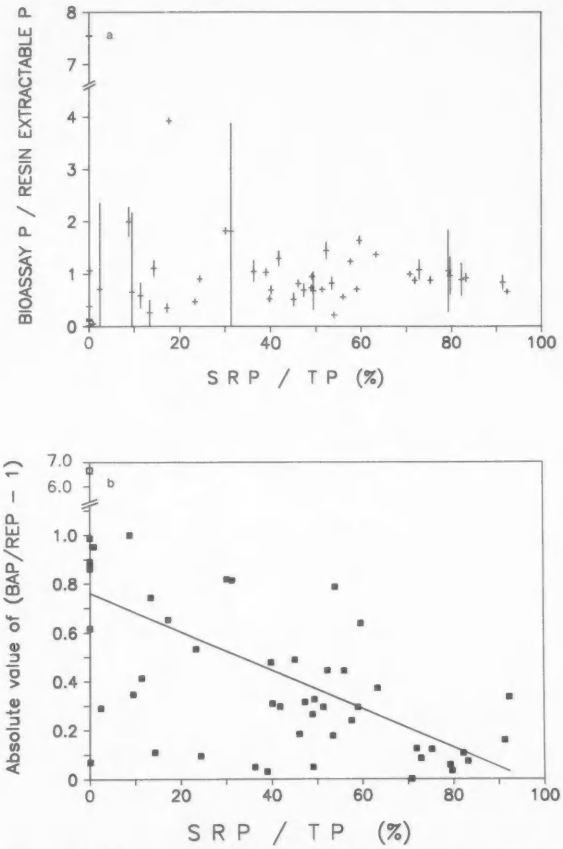

FIG. 4. (a) Ratio BAP:REP as a function of SRP expressed as a percentage of TP. The vertical lines represent the approximate 95% confidence limits for the ratio BAP:REP. (b) Relationship between the residual of the ratio BAP:REP and SRP expressed as a percentage of TP.

from the Saune, Marcaissonne, and Hers rivers (longitude = 1.26°E, latitude = 43.37°N) draining agricultural watersheds, 19 wastewater effluents (activated sludge, trickling filters, and rotating biological contactors), 22 industrial effluents ranging from food processing plants, chemical industries to detergent manufacturers, and eight tannery effluents. All sites are located in Southern France.

Statistical Analyses

All statistical analyses were carried out using Statistix commercial package.

Results and Discussion

Table 1 summarizes the descriptive statistics of the data. Total phosphorus values differ by four orders of magnitude and the difference between mean and median show that the data are not normally distributed, due to the high values typical of industrial or wastewater effluents. Total soluble phosphorus concentrations follow the same trend. In natural waters and wastewater treatment plant effluents, most of the TSP is SRP, but in most tannery effluents, SRP tends to be negligible. By far, the high-

TABLE 2. Proportion of samples (percent of samples from different origins) according to the percentage that resin extractable P (REP) represents relative to bioassay available P (BAP): REP represents more than 120% BAP (BAP<REP), REP varies from 80 to 120% BAP, (BAP = REP), and finally, REP is less than 80% BAP (BAP > REP).

	Natural waters	Wastewater effluents	Industrial effluents	Total
BAP<REP	33	47	55	48
BAP=REP	33	47	23	34
BAP>REP	33	5	23	18
Total	18	38	44	100

est P concentrations for all P fractions were measured in two samples originating from a detergent manufacturer.

Comparison Between Resin Extractable P and Bioassay P

If one influential outlier is excluded (Cook's criterion, Cook 1977), the overall correlation between the logarithms of resin extractable P (REP) and algal assay P (BAP) values (Fig. 3) is:

$$(1)\quad \text{Log}_{10}\,\text{BAP} = 1.046\,\text{Log}_{10}\,\text{REP} - 0.285,$$

($r^2 = 0.834$; $n = 49$; $s^2 = 0.1655$). The intercept and the slope do not differ significantly from zero and unity, respectively, indicating that REP, on the average, approximates bioavailable P. Huettl et al. (1979), also found that the amount of inorganic P extracted by an aluminum-saturated strong-acid cation exchange resin averaged 98% of that available to algae in bioassays.

Although the resin extracted an average 92% of BAP, the ratio of BAP:REP varied greatly among individual samples. To compare the two estimates, approximately 95% confidence limits for the ratio BAP:REP were calculated following Colquhoun (1971). This procedure generates conservative statistical limits that often indicate significant differences between very similar bioassay and resin extraction estimates (Fig. 4a). The estimates were considered similar only when the amount of P extracted by the resin was within the approximate 95% confidence limits of bioassay P.

Excluding industrial effluents for the moment, bioassay and resin extracted similar quantities in 41% of the samples. The resin extracted more than did the algae in 40% of the samples and less in the remaining 19% (Table 2). The two estimates are more similar in samples where SRP represents a large proportion of TP; this is shown more clearly by a plot of the residuals of the ratio BAP:REP against SRP (Fig. 4b). In waters with high SRP:TP (SRP >40% TP), orthophosphate usually represents a substantial part of P, whereas in samples with low SRP:TP, orthophosphate represents less than 40% TP. In low SRP:TP waters, the difference between resin extraction and bioassay can be very large, suggesting that resin extraction tends to be more reliable for waters containing relatively large proportions of SRP and presumably PO_4. The smaller the proportion of SRP, the larger the fraction of more complex organic P compounds that may not be solubilized in the 24-h extraction period or may behave less predictably than SRP. For the 20 samples having SRP <40%, the resin extracted more P than was bioavailable in 10 samples, less in four and the same amount in six. However, 13 out of the 14 for which REP differed from BAP originated from industrial effluents containing either complex P compounds which may be biologically available over the longer term or toxic substances which may inhibit algal development.

TABLE 3. All possible subset $\log_{10}$–$\log_{10}$ regression models for bioassay available P (BAP) including the following variables: total P (TP), total soluble P (TSP), soluble reactive P (SRP), and resin extractable P (REP). Listed are the number of parameters in the model including β_0 (p), Mallows C_p statistic, the correlation coefficient (r^2), and the residual mean square (s^2).

P	C_p	r^2	s^2	Model variables			
1	506.5	0.000	0.979	Intercept only			
2	65.6	0.802	0.198	TP			
3	52.4	0.829	0.175	TP	TSP		
4	7.2	0.915	0.089	TP	TSP	SRP	
5	5.0	0.922	0.083	TP	TSP	SRP	REP
2	52.3	0.826	0.174		TSP		
3	10.9	0.904	0.098		TSP	SRP	
2	97.9	0.743	0.257			SRP	
3	6.1	0.913	0.089	TP		SRP	
4	3.4	0.922	0.082	TP		SRP	REP
3	3.0	0.919	0.083			SRP	REP
2	36.5	0.854	0.146				REP
3	38.5	0.848	0.149	TP			REP
4	34.5	0.865	0.141	TP	TSP		REP
3	34.6	0.861	0.142		TSP		REP
4	3.3	0.922	0.082		TSP	SRP	REP

Cowen and Lee (1976) have suggested that resin extracts available P in waters with low SRP levels, but underestimates available P in waters with higher levels, because excessive SRP saturates resin exchange sites. In contrast to those expectations, my resin extraction technique underestimated the BAP of only 1 of 14 samples containing more than 5 $mg \cdot L^{-1}$ SRP. Apparently, saturation was successfully avoided by controlling the concentration of loaded salts.

Reduced adsorption by the resin at high concentrations of SRP could also reflect a disequilibrium between the solid and liquid states. Because the particles settle out in the sample loop of my experimental set-up, release from natural particles and sorption by the resin take place in separate units. Water flowing through the exchanger bed contains only P liberated during the preceding cycle. Recycling of the solution through the system for 24 h allows for 48 successive flowthroughs and therefore promotes liberation of P from particulate or organic phases to the water thus enhancing P adsorption by the resin. As a result, the resin extracted more P than was initially present as SRP in 76% of the samples.

The resin extracted less P than was initially present as SRP for 22% of the samples. Several authors (Rigler 1968; Downs and Paerl 1978; Huettl et al. 1979 suggest that organically bound PO_4 is hydrolyzed by the acidic molybdate reagent and that SRP thereby overestimates both PO_4 and anion-exchangeable P.

Comparison with Other Estimators of Bioavailability

All possible subset regression analyses was performed after removal of two outliers. The resulting regressions were assessed according to the following criteria: the coefficient of determinism (r^2), the residual mean square (s^2), and Mallow's C_p statistic which is an index of the bias in the fitted response values (Table 3). "Good" models have C_p values near, or less than p, the number of parameters in the model including β_o (Draper and Smith 1981).

The logarithmically transformed values of BAP (Y) were regressed against those of REP and each of the most common P fractions (TP, TSP, SRP) proposed to estimate P bioavailability (X), using least squares regression. Although BAP gave

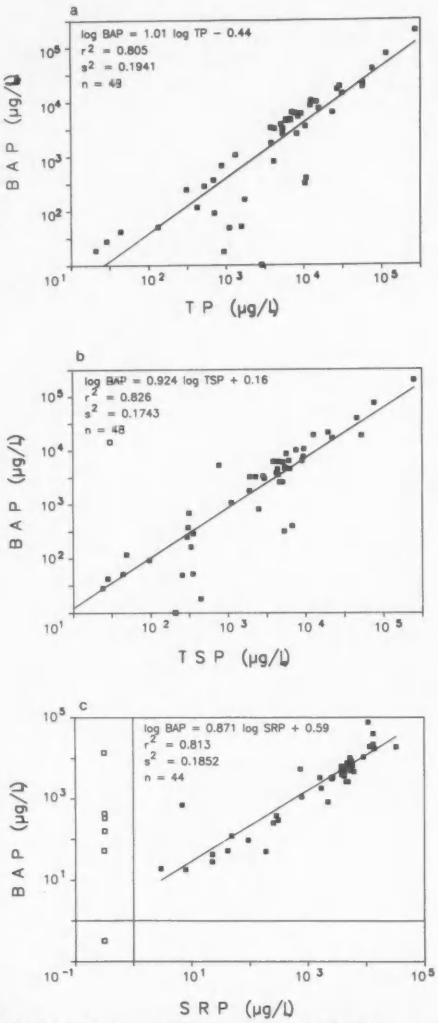

FIG. 5. Relationship between BAP and: (a) total P (TP) concentrations; (b) total soluble P (TSP) concentrations; (c) soluble reactive P (SRP) concentrations.

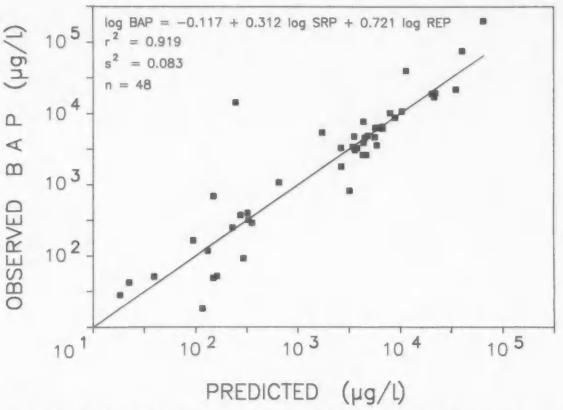

FIG. 6. Relationship between observed BAP and bioavailable P predicted by the model combining resin extractable P (REP) and soluble reactive P (SRP).

the highest adjusted r^2 when correlated with REP, this correlation is not significantly better (F-test $p=5\%$) than those between bioavailability and any other P fraction ($r^2=0.743$ to 0.826), nevertheless, it represents the least biased regression ($C_p=36.5$).

Good correlations between BAP and resin extractable P and other chemically determined fractions do not imply that these fractions adequately estimate bioavailability. The equivalence between any variable and BAP was determined by whether or not the value of the predictor variable fell within the approximate 95% confidence limits of BAP (Colquhoun 1971).

Total phosphorus overestimates BAP in 68% of the samples (Fig. 5a) and on average, BAP amounts to only 58% of TP (Table 1). Although present practice in nutrient-response regressions and loading models implies that TP adequately predicts bioavailable P (Peters 1986), this is not so. The large residual variation in these regressions would perhaps be reduced if a measure of biologically available P replaced TP.

Total soluble phosphorus also overestimates bioavailability, but to a lesser extent. On the average, BAP accounted for 86% of the TSP pool (Fig. 5b), a figure similar to those of Bradford and Peters (1987) and Broberg (1983), who found that bioavailability represented 80 and 78% of TSP, respectively. Bradford and Peters (1987) found that TSP is the best predictor of bioavailability among several P fractions that did not include resin extraction. My data support their conclusion since TSP is the best predictor after resin extraction (Table 3).

The amount of BAP was generally higher than the initial concentrations of SRP (Fig. 5c). On average, BAP represented 256% of SRP and the algae extracted more P than was initially present as SRP for 46% of the samples and less for only 10% of them. Soluble reactive phosphorus gives a conservative estimate of BAP and this underestimate is enhanced at lower SRP concentrations (Fig. 5c). A number of studies (Rigler 1975; Downes and Paerl 1978; Peters 1979; Stainton 1980; Tarapchak and Rubitschun 1981; Twinch and Breen 1982; Nürnberg and Peters 1984) have already shown that SRP is not always a good estimator of available P.

It is also possible that bioavailability is best predicted by some complex function of these subfractions. On the basis of the C_p statistic (Table 3), the preferred model is:

$$(2)\quad \mathrm{Log_{10}\ BAP} = -0.117 + 0.312\ \mathrm{Log_{10}\ SRP} + 0.721\ \mathrm{Log_{10}\ REP},$$

($r^2=0.919$; $n=48$; $s^2=0.083$ and $C_p=3$ for $p=3$) (Fig. 6). The residual variance is significantly reduced relative to equation (1) (F-test, $p=5\%$). Moreover, this model provides the overall C_p value closest to p, the highest adjusted r^2, and smallest s^2 among two- and three-parameter models. The addition of further variables in the regression equation removed less than 0.11% of the unexplained variation in the response.

Conclusion

This study demonstrated that the P extracted by the resin in this experimental set-up provides the least biased approximation of the P fraction available for algal growth over incubation periods of up to 3 wk. Resin extraction can be reliably used for

natural waters, wastewater treatment plant effluents, and waters with high inorganic P contents. Resin extraction is easily adapted for routine monitoring, the results are quickly obtained relative to bioassays, and this technique does not induce major changes in the chemical constitution of the water sample.

Nevertheless, the technique has certain limitations. In 18% of the samples, resin extracted less P than did the bioassay, and it must be presumed that the algae can use some P fraction that is not absorbed by the resin. Resin extraction results should be interpreted cautiously for industrial effluents or other waters where toxic effects might be expected to reduce algal growth.

Within the scope of this study, the model using REP and SRP is the most effective estimator of P bioavailability. Since this model is the most adequate statistically, since resin extraction is far less time-consuming than bioassays, and since SRP is analyzed routinely, the REP-SRP model offers a realistic alternative for the determination of P bioavailability.

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Proximate Analysis of Fish Tissue by Mid-Infrared Transmission Spectroscopy

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Mid-infrared spectroscopy was assessed as a means for rapidly determining the fat, protein, and moisture content of fish tissues. For fat and protein, a sample preparation protocol was developed for the conversion of fish tissue into a milk-like emulsion for analysis by a Multispec MK 1 infrared milk analyser. Fish (cod, tuna, and mackerel) were minced, dissolved, and emulsified in 0.2 M NaOH using a polytron and analysed for fat and protein using the conventional fat and protein wavelengths used for milk analysis. Instrument calibration for fat and protein was based on the Mojonnier and Kjeldahl procedures, respectively. Moisture was determined separately by extracting the water from the minced tissue using absolute methanol and measuring the absorbance of the resulting solution using a 5.56/6.02-μm filter pair. The instrument was calibrated using standardized water–methanol mixtures and the results compared with the standard vacuum oven method. Rapid analyses of fat and protein were possible giving individual results to within 1% of the standard chemical determinations. Moisture analysis, also worked well, being more accurate and rapid than the vacuum oven procedure. The limiting factor in its use for proximate analysis appears to be a combination of sample compositional variation and/or the general reproducibility of the standard methods. We conclude that the analysis of fish by mid-infrared transmission spectroscopy could serve as a means of rapidly carrying out the proximate analysis of fish and fish products for quality control purposes.

L'utilité de la spectroscopie en infrarouge moyen comme façon de déterminer rapidement la teneur en gras, en protéines et en humidité des tissus de poissons a été évaluée. Pour le gras et les protéines, un protocole de préparation des échantillons a été mis au point pour la conversion des tissus de poissons en une émulsion lactée qui sera analysée au moyen d'un appareil d'analyse infrarouge du lait Multispec MK I. Le poisson (morue, thon et maquereau) a été haché, dissout et émulsifié dans une solution 0,2 M de NaOH à l'aide d'un polytron; la teneur en gras et en protéines a été déterminée par l'utilisation des longueurs d'ondes du gras et des protéines utilisées généralement pour l'analyse du lait. La calibration des instruments pour déterminer la teneur en gras et ne protéines a été faite à l'aide, respectivement, des procédés Mojonnier et Kjeldahl. L'humidité a été déterminée à part par l'extraction d'eau du tissu haché avec du méthanol pur; l'absorbance de la solution a été mesurée au moyen de deux filtres de 5,56/6,02 μm. L'instrument a été calibré à l'aide d'un mélange d'eau et de méthanol normalisé et les résultats comparés à la méthode normalisée de l'étuve sous vide. Il a été possible d'analyser rapidement la teneur en gras et en protéines et les résultats individuels obtenus étaient à moins de 1 % des déterminations chimiques normales. L'analyse d'humidité a également bien fonctionné, étant plus rapide et plus précise que la méthode de l'étuve sous vide. Le facteur qui en limiterait l'utilisation comme analyse approximative semble être une combinaison de la variation de la composition de l'échantillon et/ou de la reproductibilité générale des méthodes normales. Les auteurs concluent que l'analyse du poisson par la spectroscopie de transmission dans l'infrarouge moyen pourrait être utilisée pour analyser approximativement et rapidement les poissons et les produits du poisson à des fins de contrôle de la qualité.

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The successful application of mid-infrared transmission spectroscopy to the rapid and quantitative analysis of milk has had a tremendous impact on the dairy industry in the industrialized world (Biggs 1967; Grappin and Jeunet 1976). The speed of multicomponent analysis of fat, protein, and lactose along with its sound correlation with the more time consuming standard chemical methods has led to its world-wide adoption for producer payment (van de Voort 1980) and dairy herd improvement work (van de Voort et al. 1987). Aqueous infrared transmission spectroscopy is based on the absorption of infrared energy at specific wavelengths by functional groups such as the carbonyl group in the ester linkage (5.73/5.58 μm) of fat or the peptide bond (6.46/6.68 μm) of proteins. Although water interferes significantly in the mid-infrared region of the spectrum, modern interference filter instrumentation, using a narrow (~40 μm) calcium fluoride cell, a short optical path, and sensitive infrared detectors are capable of overcoming this formerly formidable limitation. To date these instruments have been specifically designed for milk analysis; however, the potential exists to expand the use of this methodology to other food systems. Some of the applications investigated in our laboratory include the analysis of fat and protein in meat products (Mills et al. 1983, 1984), the study of sugars (Mills et al. 1986), ammonia in Kjeldahl distillates (van de Voort et al. 1986), and

the development of a method of moisture analysis (van de Voort et al. 1988).

Canada is a leading world exporter of fish and is in the process of diversifying its processing operations to produce more value added products rather than simply exporting the raw material. The success of surimi and related products has led to the concept of using fish tissue as a base component for producing new value added products and offers new ways to make use of underutilized species. Mechanical deboners and more efficient processing techniques have also reduced waste and allowed more fish flesh to be recovered, which in turn can be formulated into products such as fish patties, fish balls, and other reformed products. The moisture content of fish affects its stability, processing characteristics, and retail value and can vary substantially with season and reproductive cycle (Love 1979). The fat portion is a complex mixture of triglycerides, phospholipids, and other minor lipid constituents, the total content of which is also highly variable and its determination is crucial for the assessment of fish stability (suceptibility to autoxidation) during frozen storage, adjustments for processing requirements (canning), and nutritional labeling (ANON 1979). Protein is the main functional and nutritional component of fish tissue and also varies considerably within and between species (Konosu 1974). The manufacture of formulated processed products, requires more stringent raw material quality control assessment and most commonly involves the analysis for fat, protein, and moisture. Conventional methods for the determination of these components, i.e. vacuum oven for moisture, the Bligh and Dyer (1959) for fat and the Kjeldahl for protein are slow and time consuming.

The proximate analysis of food products, including fish, is an ongoing concern and expense in the food industry. Previous work had shown that mid-infrared transmission analysis could be used to determine fat and protein in raw and processed meat (Bjarno 1981, 1982; Mills et al. 1984). The success of surimi, its related products, and the more efficient use of mechanically deboned fish tissue in formulated products requires that more consideration be given to ensuring and/or adjusting the uniformity or composition of the raw material. Substantial research is being done to simplify or automate proximate analyses of food to minimize the labour and time factors associated with the traditional standard methods. Near infrared spectroscopy has made the greatest strides in this regard (Williams and Norris 1987), while mid-infrared spectroscopy has dominated milk analysis, but has not seen widespread development for other products. The mid-infrared portion of the spectrum has the advantage of being more specific in its measurement, since it is based on the measurement of fundamental wavelengths rather than overtones. Clearly sample preparation is potentially a bottleneck, however the conversion of samples to a milk-like emulsion is not complicated and is possible for many food systems. This paper reports on the development, assessment, and application of mid-infrared transmission spectroscopy as a means of providing proximate analysis (fat, protein and moisture) data for fish tissue.

Materials and Methods

Instrumentation

A Multispec MK I infrared milk analyser (Biggs 1979a) was used for this work, modified only by placing a water wavelength filter pair (van de Voort et al. 1988) in the CH stretch wavelength slot on the filter wheel (Mills and van de Voort 1982). The instrument was connected to a HP-85 microcomputer to process the uncorrected instrumental signals via a multicomponent calibration equation into its final corrected form. After zeroing the instrument against water, the fat and protein channels were linearized using standard solutions of 1,4-butyrolactone and calcium propionate while for moisture, the instrument was zeroed against dry methanol and linearized using water–methanol mixtures.

Fat and Protein

Three types of fresh fish, tuna, mackerel, and cod were purchased locally, minced twice through a 3.2-mm plate, mixed thoroughly, subdivided into homogeneous packets of approximately 50 g each and individually placed in zip-lock bags. The sample bags were frozen in liquid air and stored at −18°C for use as required. For fat and protein analysis, the sample preparation protocol previously used for meat products (Mills et al. 1984) was modified slightly (0.20 M NaOH and 85°C) to convert the minced fish tissue into a stable milk-like emulsion. The basic process involves the weighing of ~20 g of minced fish into a tarred 500-g beaker, the addition of one drop of antifoam, followed by ~150 g of preheated (85°C) 0.2 M NaOH, after which the tissue was disrupted and emulsified for 4 min at high speed using a polytron (Brinkman Instruments Ltd). After blending, the polytron stem is rinsed with warm 0.2 M NaOH using a squeeze bottle and the weight brought to 200 g with the same solution. All operations are carried out on an accurate weight/weight basis (two place top loading balance) to ensure simplicity of preparation and to maintain quantification. As a precaution to prevent blockage of the 40-μm calcium fluoride cell, the prepared emulsion was strained through a small (8 cm in diameter) stacked triple sieve set (sieve order 100, 150, 325-mesh, respectively) held in a buchner funnel to allow passage of the solution into a 300-mL screw capped container. Prior to analysis, the sample container was placed in a 40°C water bath to match the operating temperature of the infrared instrument, inverted several times to mix the sample and pumped through the instrument. The resulting emulsion is generally grey-brown to milk-like in appearance depending on its fat content and is handled in a manner similar to milk.

Because the infrared milk analyser is a secondary method of analysis, it requires calibration against primary standard methods (van de Voort 1980). To prepare appropriate material for calibration purposes, minced fish tissue was chemically analysed to determine its fat and protein content. Based on this information the total solids content of the calibration solutions were adjusted and/or samples mixed to obtain a range of values for fat and protein. The chemical analyses for the calibration were carried out on the prepared emulsions rather than the tissue because previous work (Mills et al. 1984) indicated that direct tissue analyses were not sufficiently representative of the material presented to the instrument. Twelve preanalysed samples were used for the calibration (Biggs 1979b) which were split, with half the sample being assessed instrumentally, while the other half was analysed chemically. Protein determinations were done by micro-Kjeldahl (AOAC 1980) using a 6.25 conversion factor for nitrogen to protein, while the fat content was determined by Mojonnier (Mills and van de Voort 1982). The chemical data were processed in relation to the uncorrected instrument signals for fat and protein using multiple regression (Statgraphics 1985) to derive two multicomponent calibration

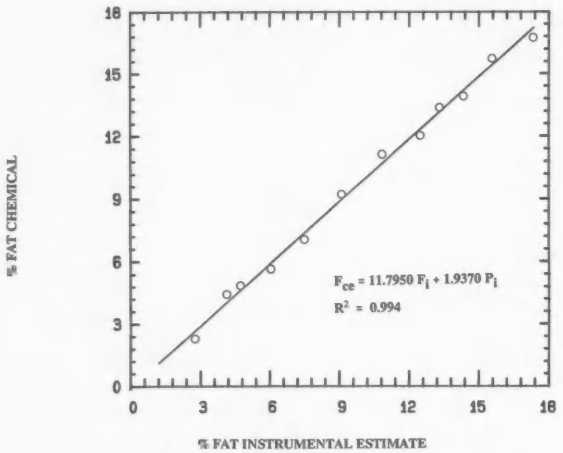

FIG. 1. Plot of predicted chemical estimates for fat versus the respective chemical analysis as determined by the multicomponent calibration equation (1).

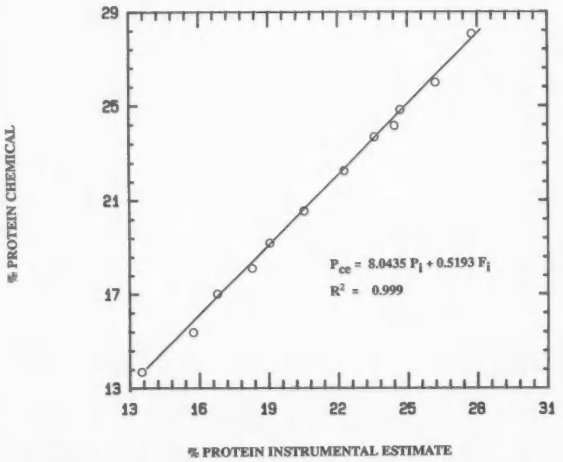

FIG. 2. Plot of predicted chemical estimates for protein versus the respective chemical analysis as determined by the multicomponent calibration equation (2).

equations, which in turn were used to calculate chemical estimates for the solutions analysed by the instrument. Comparative data analysis was carried out using the techniques outlined in the statistical manual of the AOAC (Youden and Steiner 1975).

Moisture

For moisture analysis similar fish samples prepared for fat and protein analysis were used. After thawing, the samples were split, four portions taken for moisture analysis by the vacuum oven method (AOAC 1980) and the remainder used for the methanol extraction procedure and subsequent infrared analysis. To produce fish samples which varied significantly from the original moisture content, selected samples were placed above saturated salt solutions in desiccators which generated specific relative humidities (van de Voort et al. 1988), which

TABLE 1. Comparative data for chemical results for fat and protein (percent) obtained by repeated preparation of emulsions from a selected lot of fish (n = 45).

	Cod		Mackerel		Tuna	
	Fat	Protein	Fat	Protein	Fat	Protein
Mean	3.05	16.02	11.87	18.22	12.80	22.30
Standard deviation	0.43	0.86	0.92	0.66	0.88	0.98
Range	0.89	2.23	2.13	1.90	1.63	2.30

TABLE 2. Comparative data for instrumental results for fat and protein (%) obtained by repeated preparation of emulsions from a second selected lot of fish (n = 45).

	Cod		Mackerel		Tuna	
	Fat	Protein	Fat	Protein	Fat	Protein
Mean	3.14	15.27	12.59	17.29	10.48	21.08
Standard deviation	0.20	0.43	0.64	0.55	0.42	0.57
Range	0.55	1.14	2.27	2.05	1.42	1.87

gradually adjusted the moisture content of the minced fish to new values. By using this technique a wide range of moisture contents could be generated. To calibrate the infrared milk analyser for moisture measurements, calibration standards were prepared by adding distilled deionized water to absolute methanol (kept dry over molecular sieve) on a weight/weight basis (~0–10%), which in turn were stored in screw capped glass bottles for use as needed. The water channel was zeroed against absolute methanol, the standards pumped through the instrument and the resulting water signals recorded. The signals produced by the solutions were plotted against percent moisture to produce a standard curve.

For the extraction of moisture using dry methanol, a series of large (40 mL) screw capped centrifuge tubes were prepared. To each, approximately 1 g of fish was added, followed by ~30 mL of dry methanol delivered by re-pipette, the test tube capped and placed for 10 min in a vigorously shaking water bath held at 60°C. The tubes were then removed from the water bath, centrifuged for 2 min at maximum speed to remove any suspended matter and the clear supernatant pumped through the infrared milk analyser (approximately four pumpings). To ensure good quantification, all operations require the accurate recording of the weights of fish and methanol. By writing a short APL (a programming language) program which makes use of the calibration equation and the weights of methanol and fish, the moisture content of the original sample was readily calculated.

Results and Discussion

Fat and Protein

The sample preparation protocol developed for meat products (Mills et al. 1984), modified only in terms of the concentration of base (0.2 M NaOH versus 0.1 M) and an increase in solution temperature (85°C versus 70°C) worked well in producing a homogeneous emulsion for the fish investigated. Some foaming was encountered; however, this was minimized by the use of a small amount of antifoam which was not found to interfere with the instrument signals at the levels used. Using multiple

TABLE 3. Comparison of the mean of the instrumental chemical estimates of mixed fish samples to the mean chemical values of the same samles for fat and protein (n = 33).

	Fat	Protein
Chemical mean	10.95	20.46
Instrumental mean	10.54	20.43
Mean difference	0.41	0.03
Standard deviation of difference	0.97	0.84

regression, the chemical data from the preanalysed calibration samples were related to the uncorrected instrumental signals for fat and protein to derive two calibration equations used to calculate the instrumental chemical estimates.

(1) $F_{ce} = 11.7950F_i + 1.9370\,P_i, \quad r^2 = 0.994,$
$SEE = 0.878, MD = 0.038, SDD = 0.810.$

(2) $P_{ce} = 8.0435P_i + 0.5193F_i, \quad r^2 = 0.999,$
$SEE = 0.674, MD = -0.026, SDD = 0.694.$

Where F_{ce} = Fat instrumental chemical estimate, P_{ce} = Protein instrumental chemical estimate, F_i = Fat instrumental signal, P_i = Protein instrumental signal, r^2 = Correlation coefficient, SEE = Standard error of the estimate, MD = Mean difference between chemical data and instrumental estimate, SDD = Standard deviation of the difference between chemical and instrumental estimate.

Figure 1 and 2 illustrate the relationship of the chemically estimated values (least squares regression line) obtained using equations (1) and (2) in relation to the chemical data for fat and protein, respectively. This type of data has traditionally been assessed using the method proposed by Youden and Steiner (1975) using mean differences (*MD*) and standard deviation of the differences (*SDD*s) in terms of accuracy (chemical data in relation to instrumental data) and reproducibility (in terms of duplicate chemical or instrumental values). Equations (1) and (2) do not fully meet the standards suggested for milk calibrations (Biggs 1979b) which are specified in terms of accuracy as having a $MD <= 0.05\%$ and $SDD <= 0.06\%$. The *MD*s of 0.038 and −0.026% for fat and protein indicates that the calibration is good on average and meets the milk analysis specifications; however, the *SDD*, or the spread around the differences is ten-fold higher than milk specifications, indicating a greater variability in the individual results. Subsequent analysis of 50 duplicate sample readings, representative of the three fish species, without reference to chemical analysis, produced *MD*s of −0.03 and −0.04%, and *SDD*s of 0.19 and 0.21% for fat and protein, respectively in terms of instrumental reproducibility. Once again, on average the mean differences were close to specifications overall; with the *SDD*s being about one-third of the chemical/instrumental comparison, but still about one magnitude greater than milk specifications.

Forty-five samples were taken from the same lot of each fish species, emulsions were prepared and subsequently analysed chemically for fat and protein (Table 1). By averaging the fat and protein standard deviations, the chemical results vary ±0.73 and ±0.83%, respectively with the individual range values providing an indication of maximum spread encountered in the values from the lot. Instrumental data from a second lot of fish samples, had an averaged standard deviation of ±0.42 and ±0.52% for fat and protein, respectively (Table 2). The data obtained for the two lots are generally comparable,

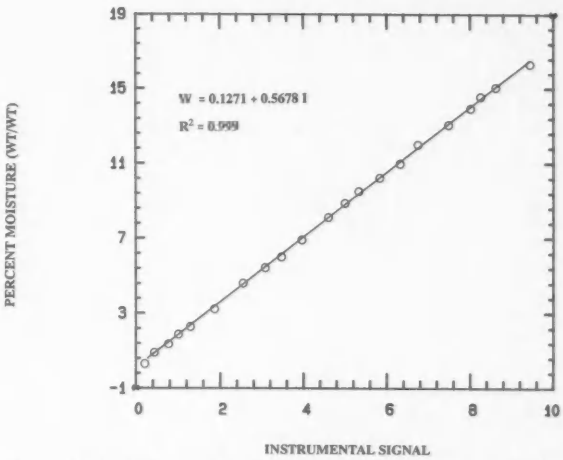

FIG. 3. Calibration curve of percent moisture versus instrument signals obtained for the water channel for water–methanol mixtures.

however, the *SD* of the instrumental results is lower overall, indicating that the instrumental data is less variable relative to the chemical methods. With the exception of the cod results, which are slightly high, the chemical and instrumental results were in line with the ranges found in the literature (Sohn et al. 1961). The instrument may not be a limiting factor, but rather sample preparation, chemical analysis, the inherent sample variability and/or a combination of these variables may limit the accuracy and reproducibility of the infrared method. These limiting factors are superimposed on the resultant instrumental chemical estimates and as a consequence the standard deviation can become a significant factor when the fat or protein content at the lower end of the scale are assessed. We compared the means of the chemical estimates obtained instrumentally to the means of samples checked chemically immediately after instrumental analysis (Table 3). This assessment includes all the cumulative sources of variability; chemical, sample, and calibration. On average the protein data is similar, while the fat results are slightly low (0.41%), with the *SD* around the differences being in the order of 1%. These values can be compared to the previous meat study (Mills et al. 1984), where *MD* and *SDD* values for fat and protein were 0.21; 0.13% and −0.10; 0.45%, respectively. Averaging out all the chemical *SD*s from Table 1 (~0.78%) and those in Table 3 for accuracy (0.91%) indicates that the infrared method could be a reasonable substitute for the chemical procedures for quality control purposes, but not for analysis requiring a high degree of accuracy.

Moisture

The basic principles and development of using mid-infrared transmission spectroscopy to determine moisture has been discussed in a previous publication (van de Voort et al. 1988) and was based on the initial near infrared work by Goulden and Manning (1967). The basic premise was to take advantage of the high sensitivity of the mid-infrared portion of the spectrum to moisture by extracting it into a hygroscopic solvent such as methanol which does not interfere with the strong water absorption band at 6.02 μm. Previous work had concentrated on low moisture products such as skimmilk powder, bread crumbs, and

TABLE 4. Analysis for reproducibility of pairs (means 1 and 2) of chemical and instrumental moisture determinations ($n = 50$).

Analysis	Mean 1	Mean 2	Mean difference	Standard deviation of difference
Instrumental[a]	67.66	67.63	−0.03	0.49
Instrumental[b]	67.70	67.58	−0.12	1.19
Vacuum Oven[c]	67.75	67.07	−0.68	1.52

[a]Duplicate readings of same sample.
[b]Duplicate readings of different samples.
[c]Duplicate vacuum oven results.

TABLE 5. Comparative data for moisture analyses by the vacuum oven and infrared methods for fish ($n = 100$).

Mean	Mean vacuum oven	Mean infrared	Mean difference	Standard deviation of difference
Cod	79.92	72.04	0.88	2.03
Mackerel	66.47	65.12	1.35	2.12
Tuna	61.28	60.37	0.92	2.83

flour, which are difficult to analyse, in relation to the vacuum oven method, the AOAC (1980) near infrared method and the Karl Fischer titration procedure (van de Voort et al. 1988).

A typical calibration curve (Fig. 3) derived using 21 water–methanol mixtures is described by the following equation:

$$(3)\quad W = 0.1271 + 0.5678I \qquad r^2 = 0.999, SE = 0.131, MD = -0.002, SDD = 0.174.$$

Where: W = Moisture content (%), I = Instrument signal.

Regular fish samples and those adjusted in moisture content using equilibrium relative humidity chambers were extracted with methanol for infrared analysis and also subjected to moisture analysis by vacuum oven. The methods were first assessed for their relative reproducibility (Table 4). The *MD* and *SDD* for the instrumental method for the same sample was quite good (−0.03; ±0.49%, respectively) with the *SDD* being about half of that obtained for the fat and protein results. When individual samples were prepared and extracted, the *SDD* doubles (1.19%), indicating that inherent sample variability is contributing to the overall variability in the results. The vacuum oven method has an even greater variability, deviating substantially from the expected *MD* of zero (by −0.68%) and having a higher *SDD* (1.52%). A similar analysis was carried out comparing the instrumental data obtained for moisture with the vacuum oven method, as a function of the type of fish. Overall, the vacuum oven method gave higher results, in the order of 1% and it would appear the infrared procedure is more reproducible and may even be a better predictor of moisture than the reference method. A similar conclusion was reached when the infrared method was compared with the vacuum oven method for low moisture materials (van de Voort et al. 1988).

There are a number of limitations to the assessment of the infrared protocol developed. It is well known that the lipids of each fish species differs in its triglyceride (fatty acid) composition and that significant levels of phospholipids may be present. The response of the fat wavelength is a function of the number of ester linkages per unit weight of lipid and will vary depending on the average molecular weight. Better results can be obtained using a separate calibration for each fish species to account for this effect; however, the development of multiple calibrations would be an onerous task. The substitution of the Mojonnier procedure for the Bligh and Dyer fat analysis may also have produced a bias; however, preliminary work indicated that similar results could be obtained by both methods. In the case of protein, fish may contain significant levels of nonprotein nitrogen in the form of trimethylamine oxide, taurine peptides, amino acids, and related purine based compounds. The Kjeldahl will include these as nitrogen (converted to protein), while the infrared method will not account for these compounds. Considering the limitations indicated above, the inherent variability of the sample itself, the effects associated with the preparation procedure and the calibration, the results are quite reasonable. Overall, the method has a significant advantage in terms of analytical time even though some sample preparation is required and 10 protein results can be obtained in 1 h while a similar number of moisture analyses can be done in 20 min. The drawback to the more extensive utilization of mid-infrared technology is to a large extent the general lack of awareness of the technology, its singular association with milk analysis, and the lack of research into new applications.

Infrared analysis of fish as a means of obtaining proximate analysis data for fat, protein, and moisture appears to be feasible with a single instrument being capable of substituting for three common analytical methods with substantial time and labour savings. Combining all sources of error, it can be stated that the use of infrared transmission analysis is capable of providing results of similar accuracy as the chemical methods, but that individual analyses would provide results of ±1.0%.

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Predicting Winter Flounder (*Pseudopleuronectes americanus*) Catches by Time Series Analysis

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Jeffries, H. P., A. A. Keller, and S. S. Hale. 1989. Predicting winter flounder (*Pseudopleuronectes americanus*) catches by time series analysis. Can. J. Fish. Aquat. Sci. 46: 650–659.

Long-term changes in catches of winter flounder (*Pseudopleuronectes americanus*) were compared at five locations within Narragansett Bay, Rhode Island, USA and in three areas directly offshore. In the lower Bay, relative abundance decreased 86% during warming in the early 1970's, recovered briefly, and then declined to an all-time low in 1986. Time-series analysis successfully predicted a recovery in 1987. Year ahead predictions, based on annual models, had a maximum error of 14% (1986); monthly forecasts explained 62–72% of catch variation during the entire investigation; cumulative monthly error (forecast compared with actual over an annual cycle) was 11% in the Bay and 21% offshore. Commercial offshore catch and the fish retained on power plant intake screens in two major rivers showed the same 11-yr pattern of population fall and recovery detected in the lower Bay. Coherent behavior was also demonstrated by the similarity of random processes which generated the time-series data. Thus a single time-series model for southern New England winter flounder seems feasible.

Les variations à long terme des prises de flétan d'hiver (*Pseudopleuronectes americanus*) ont été comparées pour cinq sites dans la baie Narrangansett au Rhode Island, U.S.A. et à trois endroits directement au large. Dans la partie inférieure de la baie, l'abondance relative a diminué de 86 % au cours du réchauffement du début des années 1970, s'est rétablie brièvement, puis a diminué pour atteindre un minimum de tous les temps en 1986. L'analyse chronologique a permis de prédire une amélioration pour 1987. Les prévisions de l'année suivante, fondées sur des modèles annuels, présentaient une erreur maximale de 14 % (1986); les prévisions mensuelles ont expliqué 62–72 % au cours de toute l'étude; les erreurs mensuelles cumulatives (les prévisions par rapport à la réalité au cours d'un cycle annuel) étaient de 11 % dans la baie et de 21 % au large. Les prises hauturières commerciales et les poissons prisonniers des grilles d'alimentation des usines hydroélectriques dans deux importantes rivières ont présenté le même cycle de diminution puis d'augmentation de la population sur onze ans que ce qui avait été détecté dans la partie inférieure de la baie. Un comportement cohérent a également été démontré par la similitude des processus aléatoires qui ont produit les données chronologiques. Il semble donc possible d'élaborer un modèle chronologique unique pour le flétan d'hiver du sud de la Nouvelle-Angleterre.

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Marine fishes are usually sampled for shorter periods than the long-term environmental variations that are known to affect their abundances. This is only part of the problem in understanding the causes of population fluctuations. If progressive change, habitat degradation or climatic warming, is superimposed on a natural cycle, complexity of the situation is increased. We know little about cyclical behavior let alone its interaction with physical–chemical variation. These difficulties haunt modelers attempting to mechanistically predict abundance from simulated couplings of fluxes and compartments, an approach that is as demanding in its requirements as it is uncertain.

From 1968 to 1974, relative catch of the winter flounder (*Pseudopleuronectes americanus*) in Narragansett Bay, Rhode Island declined by 86% (Jeffries and Johnson 1976), to the consternation of fisherman and concern of biologists for the causes were not clear. A 3-yr resurgence to its former abundance (Jeffries and Terceiro 1985) was followed by a second decline terminating in 1986. This once "dominant species" had experienced a sharp decrease in abundance, and no one knew why. The causes may have been linked with climatic warming and predator control, a difficult situation for mechanistic prediction. Lacking such information, we wanted to see if population fluctuations could be predicted from long-term patterns using time-series analysis.

Winter flounder is unique among the demersal fishes inhabiting temperate East Coast waters: it spawns well within estuaries during winter–spring; larger members then swim offshore, returning in the fall to overwinter in brackish water (Saila 1961). Seasonally, the population moves opposite to the great group of visitors that enter estuaries along the Northeast coast during summer and leave in the fall. Success of the flounder's strategy is indicated by abundances ranging up to 98% of otter trawl catches.

Spawning at low temperatures appears to be an "escape in time" (Slobodkin 1962) from warm-water predators, certain members entering the estuarine environment as the flounder population leaves. It follows that warmer winters during the early 1970's (average annual warming rate 1969–75 = $0.4°C \cdot yr^{-1}$) were detrimental to the population. One hypothesis, involving a year-round resident, is that *Crangon septemspinosa*, a small shrimp reaching great abundances in Narra-

TABLE 1. Summary of data sources in and offshore of Narragansett Bay, which were used in the study.

Station name	Location	Data collection schedule	Period	Source	Data analyzed
Fox Island	41°34′N 71°24′W	weekly	1959–87	Jeffries et al. (1988)	monthly and yearly
Whale Rock	41°26′N 71°25′W	weekly	1959–87	Jeffries et al. (1988)	monthly and yearly
Mt. Hope Bay Station 1	41°42′N 71°11′W	biweekly monthly	1971–81 1982–85	Marine Res. Inc. (1972–1986)	yearly
Mt. Hope Bay Station 5	41°41′N 71°13′W	biweekly monthly	1972–81 1982–85	Marine Res. Inc. (1972–1986)	monthly and yearly
Brayton Point Power Plant	41°43′N 71°11′W	weekly	1973–85	Marine Res. Inc. (1972–1986)	yearly
Providence River Power Plant	41°49′N 71°24′W	weekly	1975–85	Marine Res. Inc., (unpubl. data)	yearly
NMFS survey Stratum 5	random stations	seasonally (spring, autumn)	1963–85	NMFS, Woods Hole, (unpubl. data)	autumn
NMFS survey Area 539	distributed	daily	1964–86	NMFS, Woods Hole, (unpubl. data)	monthly and yearly

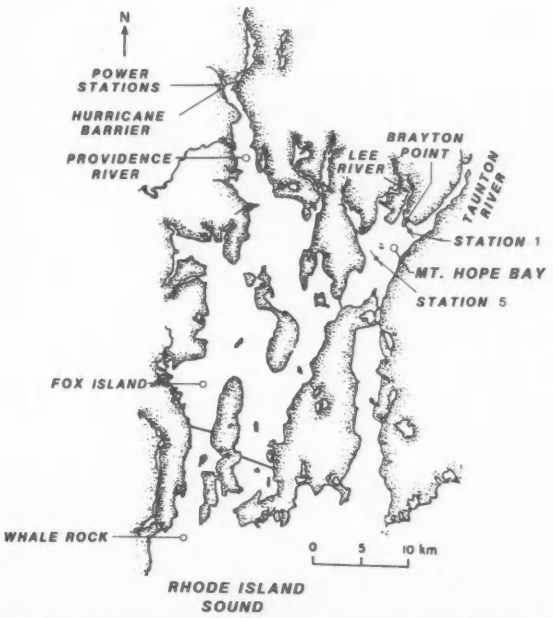

FIG. 1. Narragansett Bay and Rhode Island Sound, showing the location of sampling sites in the West Passage, Mt. Hope Bay, Providence River, and offshore.

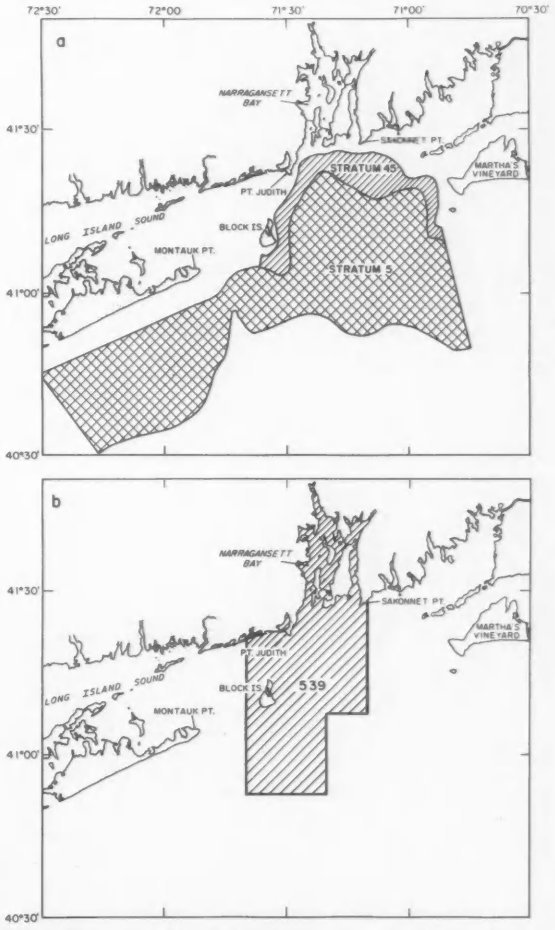

FIG. 2. Narragansett Bay and offshore waters, showing the location of National Marine Fisheries Service (a) trawl survey stratum 5, and (b) commercial catch statistical area 539.

gansett Bay, had been held in check by cold winters, but during the early 1970's warming period, it was able to feed actively on larval flounder, perhaps at the critical period when they metamorphose, fall from the plankton, and develop protective pigmentation. As winters cooled over a 3-yr period (1975–78), predation by *Crangon*, and perhaps also by small individuals of the ctenophore *Mnemiopsis leidyii* known to be present during winter, as well as by sculpins (*Myoxocephalus* spp.), was less important and the winter flounder population recovered (Jeffries and Terceiro 1985).

The population's second decline extending through the mid-1980's resulted in several trawls in lower Narragansett Bay during summer 1986 coming up without a single winter flounder.

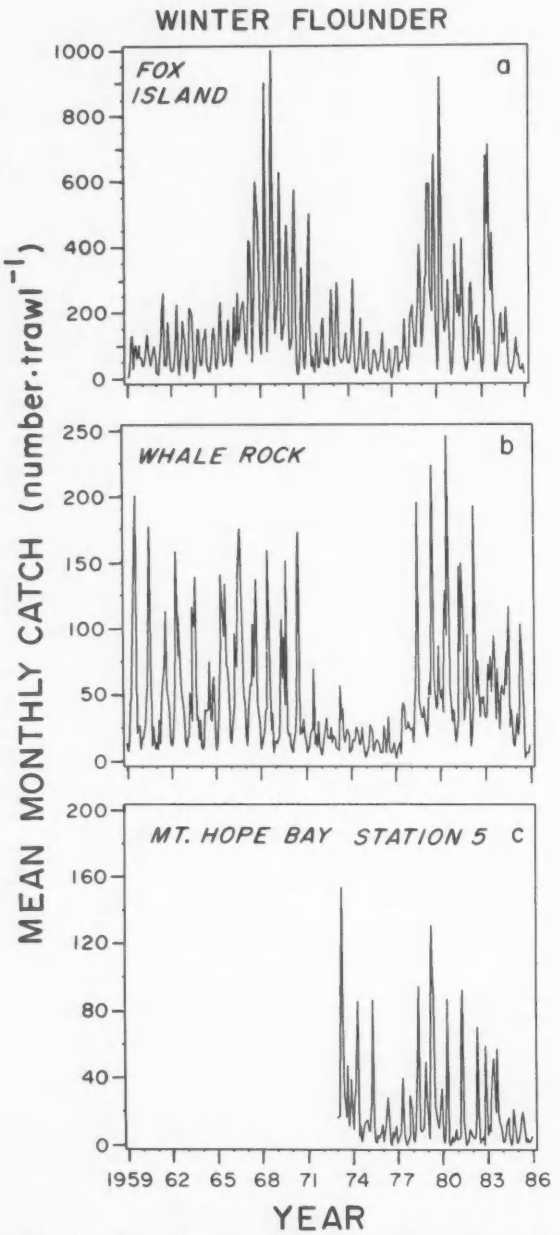

FIG. 3. Time-series of mean monthly winter flounder catch from (a) Fox Island, West Passage, Narragansett Bay (number per 30-min. trawl), (b) Whale Rock, Rhode Island Sound (number per 30-min. trawl), and (c) station 5, Mt. Hope Bay, Narragansett Bay (number per 15 min.-trawl), January 1959–December 1985.

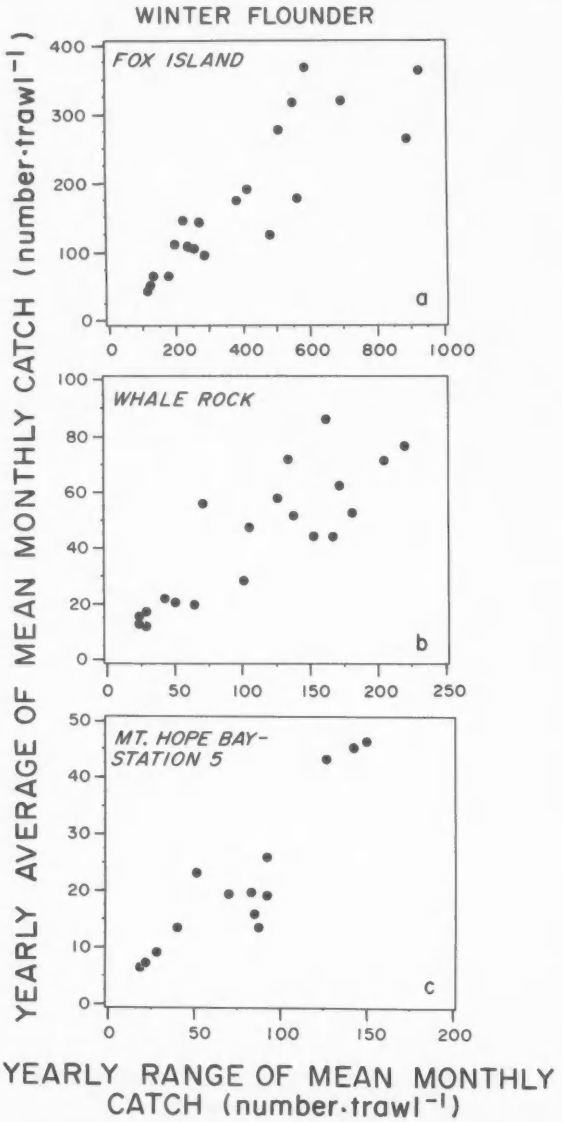

FIG. 4. Range–mean plots for mean monthly winter flounder catch from (a) Fox Island (number per 30-min. trawl), (b) Whale Rock (number per 30-min trawl), and (c) Mt. Hope Bay (number per 15 min. trawl). The ranges and means were calculated for yearly subseries, 1966–85 (Fox Island and Whale Rock), 1971–84 (Mt. Hope Bay).

The question was: is another recovery likely, based upon the population's long-term behavior, or is the situation new?

Statistical prediction can be approached in several ways (Schaefer 1954, 1957; Pella and Tomlinson 1969; Fox 1970). Time-series analysis has produced successful results with fisheries data (Boudrealt et al. 1977; Saila et al. 1980; Mendelssohn 1981; Kirkley et al. 1982; Jensen 1985; Fogarty et al. 1986; Mendelssohn and Cury 1987). We used the Box–Jenkins (1976) ARIMA (autoregressive integrated moving average) models to determine the components of cyclical behavior. Combined with correlation analysis, the final result showed similar population behavior extending throughout all of Narragansett Bay and the offshore commercial fishing areas.

Methods

Sampling

Relative abundances were estimated at a total of eight stations (Table 1, Figs. 1, 2) by otter trawl and by fish retained on power

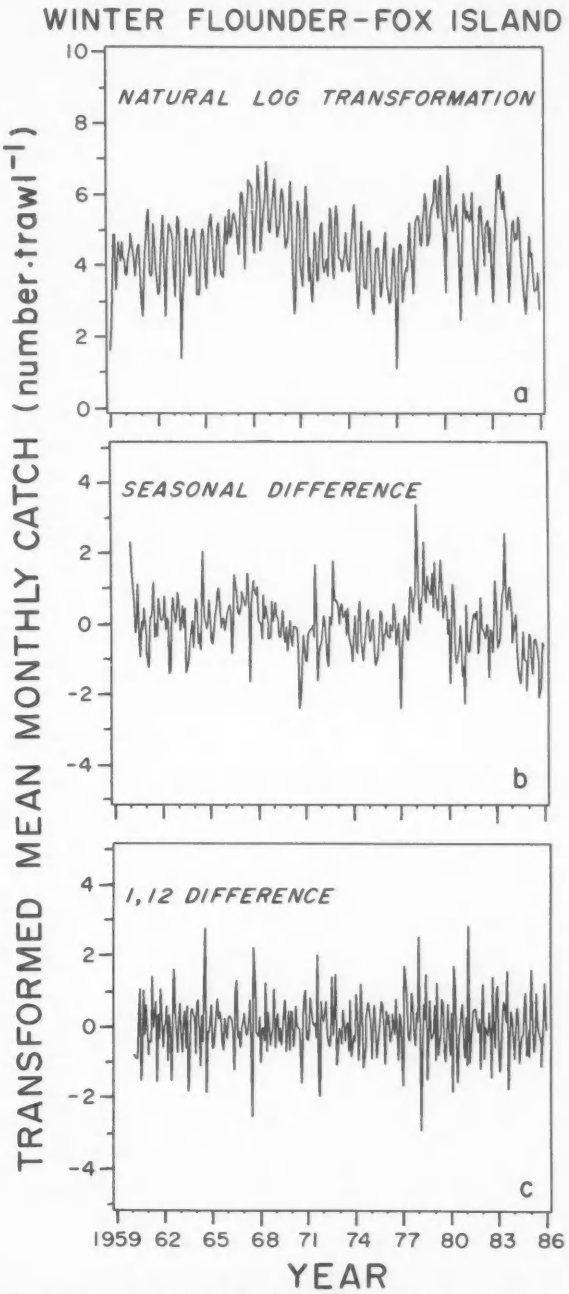

FIG. 5. Successively transformed and differenced mean monthly winter flounder catch (number per 30-min trawl) at a representative station, Fox Island, (a) natural logarithmically transformed catch series, (b) seasonally differenced (order 12) and transformed catch series, and (c) 1st and 12th differenced and transformed catch series.

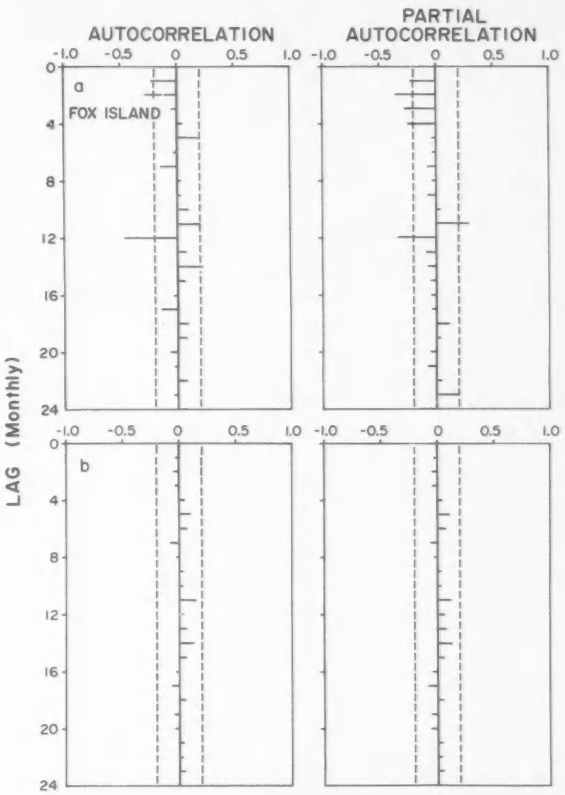

FIG. 6. Estimated autocorrelation and partial autocorrelation functions to lag 24 for (a) the transformed and differenced winter flounder catch series, and (b) the residuals of the catch model, together with their two standard error limits (broken lines) for a representative station, Fox Island.

plant intake screens: trawl stations — one in Narragansett Bay, two in the contiguous Mt. Hope Bay, one immediately adjacent in Rhode Island Sound, and two offshore; intake screen stations — single observation points in Mt. Hope Bay and the Providence River. The most intensive program was the authors' weekly otter trawl sampling, which has run from 1959 to the present in the West Passage of Narragansett Bay at Fox Island and in Rhode Island Sound, south of Whale Rock (Jeffries and Johnson 1976). The Bay station was located on the species' migratory route; the Sound station was situated as far seaward as could be visited on a regular basis. The otter trawl measured 14 m long, tapering from 10 m across at the mouth to 1 m at the throat; stretched mesh size was 7.6 cm in the forward half and 5.1 cm behind the throat. The trawl was towed at about 2.5 knots for 30 min.

The landward extreme of the population's range in Narragansett Bay was represented by sampling stations in Mt. Hope Bay and the Providence River. Since 1971, the New England Power Company has sponsored biweekly bottom trawling (Marine Research Inc. 1972–1986). Their otter trawl measured 11.4 m long with a 7.6 m head rope and an 11.1 m foot rope; stretched mesh sizes were 11.3 cm in the wings and 3.8 cm in the cod end. The net was towed at 2.0–2.5 knots for 15 min at 3–8 stations. A mid-bay station (station 5, near Spar Island) was selected for the time-series analysis. Annual catch at station 1, near the intake of the power plant, was included in a correlation analysis. The power-plant intakes in Mt. Hope Bay were typical of shore-line installations, having revolving screens (0.95-cm mesh); additional screens (3.5-cm mesh, units

TABLE 2. Parameter estimates and associated statistics for the final fitted seasonal ARIMA models at each station. The chi-square statistics are nonsignificant for autocorrelation in the residuals (through lag 24). Model: $(1-B)(1-B^{12})\ln(\mathrm{WFL}+1) = (1-\theta_1 B-\theta_2 B^2)(1-\Theta_1 B^{12})\,a_t$.

Station	Parameter	Value (SE)	n	R^2	Residual variance	Chi-square statistic
Fox Island	θ_1	0.34 (0.06)	324	0.72	0.32	15.30
	θ_2	0.33 (0.06)				(lag 24)
	Θ_1	0.81 (0.04)				
Whale Rock	θ_1	0.56 (0.06)	324	0.62	0.35	34.37
	θ_2	0.20 (0.07)				(lag 24)
	Θ_1	0.75 (0.05)				
Mt. Hope Bay	θ_1	0.51 (0.08)	156	0.63	0.61	26.74
Station 5	θ_2	0.25 (0.08)				(lag 24)
	Θ_1	0.77 (0.06)				

TABLE 3. Parameter estimates and associated statistics for the final fitted annual ARIMA models at each station. The chi-square statistics are nonsignificant for autocorrelation in the residuals (through lag 24). Model: $(1-\phi B)\ln \mathrm{WFL} = (1-\theta B)a_t$.

Station	Parameter	Value (SE)	n	R^2	Residual variance	Chi-square statistic
Fox Island	ϕ_1	0.49 (0.26)	27	0.56	0.18	19.59
	θ_1	−0.59 (0.24)				(lag 24)
Whale Rock	ϕ_1	0.50 (0.21)	27	0.69	0.10	12.41
	θ_1	−0.64 (0.19)				(lag 24)

1 and 2; 2.5-cm, unit 3) were positioned in summer to remove horseshoe crabs. We standardized abundances from 1973 to 1986 relative to volume of water pumped by three power units (Jeffries et al. 1988).

Starting in 1975, Narragansett Electric Company's Manchester Street facility in the Providence River has recorded fish caught on cooling-water intake screens. Screened wells (5.1-cm^2 mesh) were protected by revolving screens (1.3-cm^2 mesh). Abundance relative to flow could not be calculated, so we devised an index of annual abundance based on average catch per hour (Jeffries et al. 1988).

The final sampling area was directly offshore from Narragansett Bay. Since 1963, the National Marine Fisheries Service (NMFS) has sampled 2–8 randomly selected stations in stratum 5 (Fig. 2). Their spring survey entailed gear changes, so we selected the fall program, which employed a Yankee No. 36 trawl, having 12.7-cm mesh in the wings and 11.4-cm mesh in the cod end. The net's top and cod end were lined with 1.3-cm mesh net. Overall dimensions were 30 m in length, 18.3 m in headrope and 24.4 m in footrope. The net was towed on the bottom for 30 min (Grosslein 1969).

Commercial catch data from Narragansett Bay and its offings were provided by NMFS, Woods Hole for all species caught by all boats fishing in statistical area 539 from 1964 to 1986 (about 432 000 records). This included records from area 529, the area's designation from 1964 to 1967. We calculated daily catch per unit effort and made summations for monthly and annual total catches (Jeffries et al. 1988).

Time Series Analysis

Monthly time-series models were constructed for catch at Fox Island, Whale Rock and Mt. Hope Bay with the ARIMA procedure available in the Statistical Analysis System (SAS Institute 1984). Annual models (1959–85) were additionally constructed for the Fox Island and Whale Rock data. Following Jenkins (1979), a time series was defined as consecutive and consistently obtained estimates of relative population size (Y_t) that are equally spaced in time and shaped by both deterministic and stochastic events. Occasional missing data points (one value in our trawl surveys and <0.06% in the Mt. Hope Bay data) were reconstructed by linear interpolation of adjacent points.

The first step in the analysis consisted of removing deterministic trends from the series (by transformation or differencing) so that the results were stationary. To test for stationarity, series were divided into segments, and range–mean plots (Jenkins 1979) examined. Once stationary, the catch could be described as: (1) a linear combination of previous catches (an autoregressive component); (2) past values of error terms (a moving average component); and (3) the current error term. The general model, using the backshift operator, B (with $B^j X_t = X_{t-j}$), is represented as:

$$(1)\quad 1 - \phi_1 B - \phi_2 B^2 - \ldots \phi_p B^p)(1-B)^d Z_t = (1 - \theta_1 B - \theta_2 B^2 - \ldots \theta_q B^q) a_t,$$

where Z_t is the transformed and/or differenced catch (Y_t) taken at equal time intervals (t), ϕ_i and θ_i are autoregressive (AR) and moving average (MA) parameters and a_t is the error term. P is the order of the AR component, q the order of the MA component and d the degree of differencing (Box and Jenkins 1976).

Fitting a model involved the Box–Jenkins three-step procedure of identifying which terms to retain in equation (1), estimating the parameters, and checking for insignificant components and departure of the residuals from white noise. Identification and checking included examination of the autocorrelation (ACF) and partial autocorrelation (PACF) functions of the series and their residuals and comparing various models for fit.

Seasonal models were first fitted for Fox Island (Jan. 1959 to Dec. 1985), Whale Rock (Jan. 1959 to Dec. 1985), and Mt.

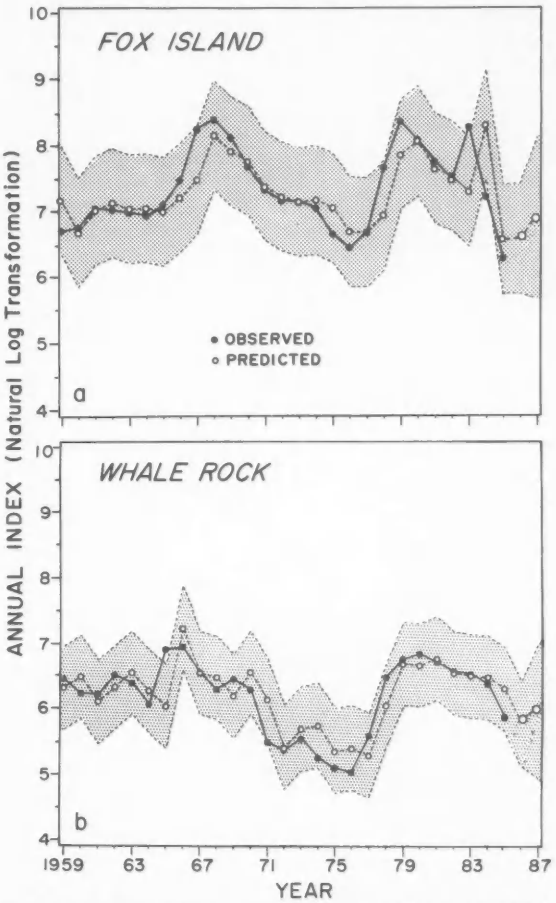

FIG. 7. Observed (solid line) versus one-step ahead forecasts and 1986, 1987 predictions (broken line) for annual indices (sum of mean monthly catch, number per 30-min. trawl) of winter flounder abundance (natural logarithmic transformation) at (a) Fox Island and (b) Whale Rock. Shaded area represents 95% confidence interval on transformed predictions.

Hope Bay (Jan. 1972 to Dec. 1984). Annual models were subsequently developed for the 27-yr catch record (1959–85) at Fox Island and Whale Rock. Goodness of fit was based on the models' coefficients of determination and the variance of the residuals. The final year of data for both annual and monthly catch was not included in the estimation of the models' parameters. These reserved data were compared with predicted values to judge the accuracy of the forecast. The observed abundance for 1987 was based on catch data through September.

Correlation

Next we used all available annual winter flounder abundances (Table 1) to compare the population's behavior throughout the entire inshore–offshore sampling area. Pearson correlation coefficients were computed among the eight stations since cross correlations (Box and Jenkins 1976) on time series with as few as 12 observations would not be meaningful.

Results

Data and Transformation (Monthly Models)

Monthly means, each representing two to five weekly samples (Fig. 3) show strong seasonality superimposed on a long-term cyclical pattern peaking in 1968 and again in 1979. There was a tendency for variance to increase with catch, so we divided the series into yearly segments and plotted the range versus the mean of each year (Jenkins 1979); these relationships (Fig. 4) indicated the need for logarithmic transformation (Jenkins 1979). We added one to catch to eliminate zero values (five values in combined data sets) and transformed abundances to the natural logarithm.

Dispersion was reduced by transformation, but seasonality persisted (Fig. 5a); we removed the seasonal trend by taking a differencing of order 12. The resultant series (Fig. 5b) still showed a cyclical trend, requiring a first-order difference of the residuals to achieve the stationary condition (Fig. 5c). Similar treatment of catch data at the two remaining stations also produced stationary series.

Model Identification, Estimation and Diagnostic Checking

A tentative model for monthly abundances was chosen based on the pattern of the ACF and PACF for the transformed and differenced winter flounder catch data. The ACF and PACF exhibited similar patterns at the three stations (see Fig. 6a for a representative sample, Fox Island). The significant negative spike at lag 2 in the ACF suggested a second-order MA model, which was confirmed by the decaying PACF pattern after lag 2. The negative spike at lag 12, in both the ACF and PACF (Fig. 6a) further indicated the need for a seasonal MA parameter. Following Box and Jenkins (1976), seasonal ARIMA models were hypothesized:

$$(2)\quad (1 - B)(1 - B^{12})Z_t = (1 - \theta_1 B - \theta_2 B^2)(1 - \Theta_1 B^S)\, a_t,$$

where $S = 12$, and Θ_1 is the seasonal MA parameter (with other parameters as previously defined).

A general nonlinear least squares fitting procedure was used to estimate the parameters of the proposed model (equation (2)) for each station. The ACF (Fig. 6a) suggested important terms at lags 5, 11, and 14. Additional models were constructed which included these terms but when tested resulted in no significant improvement in fit over the simpler model (equation (2)). The final parameter estimates (all are significant) and associated statistics for the monthly models are given in Table 2; residual ACF and PACF for Fox Island, a representative station, are shown in Fig. 6b. A chi-square test indicated that the residuals were not significantly different from white noise. The goodness of fit is indicated by the low residual variances and the high coefficients of determination for the final models (Table 2).

Annual Models

Transformation, identification, estimation, and diagnostic checking were performed on annual abundances (1959–85) at Fox Island and Whale Rock. The pattern of the ACF and the PACF suggested that a first-order, autoregressive moving average model, ARIMA (1,0,1), was appropriate for the natural logarithmically transformed abundances:

$$(3)\quad (1 - \phi B)\, Z_t = (1 - \theta B)\, a_t,$$

TABLE 4. Pearson correlation coefficients for indices of yearly abundances for winter flounder in and around Narragansett Bay, RI.

	Fox Island	Whale Rock	Station 1 MHB	Station 5 MHB	Brayton Point power station (lag 1)	Providence River power station (lag 1)	Stratum 5	Area 539
Fox Island	1.0							
Whale Rock	0.65* (<0.01)	1.0						
Station 1 MHB	0.64* (0.01)	0.35 (0.22)	1.0					
Station 5 MHB	0.44 (0.12)	0.11 (0.70)	0.79* (<0.01)	1.0				
Brayton Point power station (lag 1)	0.21 (0.51)	−0.03 (0.93)	0.80* (<0.01)	0.73* (0.01)	1.0			
Providence River power station (lag 1)	0.62* (0.08)	0.56 (0.12)	−0.04 (0.92)	0.02 (0.95)	−0.23 (0.52)	1.0		
Stratum 5	0.64* (<0.01)	0.72* (<0.01)	0.30 (0.30)	0.19 (0.52)	−0.10 (0.75)	0.83* (0.01)	1.0	
Area 539	0.64* (<0.01)	0.56* (0.02)	0.07 (0.82)	0.08 (0.78)	−0.31 (0.30)	−0.04 (0.91)	0.48* (0.04)	1.0

*($P < 0.10$)

where t represented yearly time intervals and all parameters were as previously defined. Final parameter estimates and associated statistics are seen in Table 3. The residual variances, R^2's, and chi-square statistics (Table 3) indicated that the model chosen was adequate. Once again, correspondence between observed and step ahead forecasts is very close (Fig. 7) on a logarithmic scale.

The predicted annual index of abundance (transformed) for 1986 differed from the observed by 5% at Fox Island and 14% at Whale Rock. Most important was our prediction that the size class captured by otter trawls should start to recover in 1987. The prediction is correct based upon increased relative abundance through summer 1987.

Correlation Analysis

For comparing annual catches in all eight sampling areas, we used correlation analysis (Table 4). Power plant intake screen catch was lagged by 1 yr, since large fish were excluded by coarse screens protecting the finer revolving screens from which the abundance estimates were made. A peak in small fish would not show up in trawl catches until at least 1 yr later. Strongest correlations were generally observed between adjacent areas.

Abundance patterns at significantly correlated areas ($p<0.10$) are plotted in Fig. 8. Data for the Providence River and Mt. Hope Bay power plants (trawl and intake screen catches) closely tracked the downbay pattern, including a precipitous drop in 1982, quick recovery and then decline. Offshore, a similar pattern was revealed in the NMFS fall surveys and commercial catch records.

Discussion

From eight lengthy data sets, we have described the stochastic properties of winter flounder relative abundance in the Narragansett Bay region. The population is dynamic, both seasonally and in the long-term, but because our base survey at two stations is now in its 30th year, an important prediction for 1987 could be made. We can be confident that the historical pattern and its prediction, as generated by time-series analysis, pertains not just to the two-station sampling area, but throughout the migratory range of individuals emanating as young from the Narragansett Bay and other southern New England estuaries. Moreover, we can maintain a running check on future developments within the entire population by referencing continuous monitoring programs. The approach is statistical, as opposed to inherently more satisfying deterministic models of fluxes and forcing functions, but the result here is quick and easy prediction. This is useful, both for practical purposes and for research into the causes of long-term population change.

Monthly winter flounder catch in all three areas exhibited strong annual seasonality. Points in the series were highly correlated with corresponding data at 1, 12, and 13-mo lags. Consequently, the monthly series required nonseasonal as well as seasonal differencing to achieve a stationary condition. After differencing, the population throughout Narragansett Bay was described by seasonal models with the same number and types of parameters (Table 2). Parameter values were also similar between stations. Statistically, the structure of the random processes that generated the monthly catch series was the same at two extremities of the Bay and midway along its length. A common model type was therefore suggested, indicating similarities in population dynamics and behavior throughout the Bay.

The yearly model confirmed that abundance in a given year was related to both abundance and random perturbations in the previous year. Again, both stations in the intensively surveyed lower Narragansett Bay–Rhode Island Sound area were represented by a single model type with similar parameter estimates (Table 3).

Random perturbations affected population abundance. Both the source of the perturbations and when they change direction are unknown, because interannual variation is contained in the

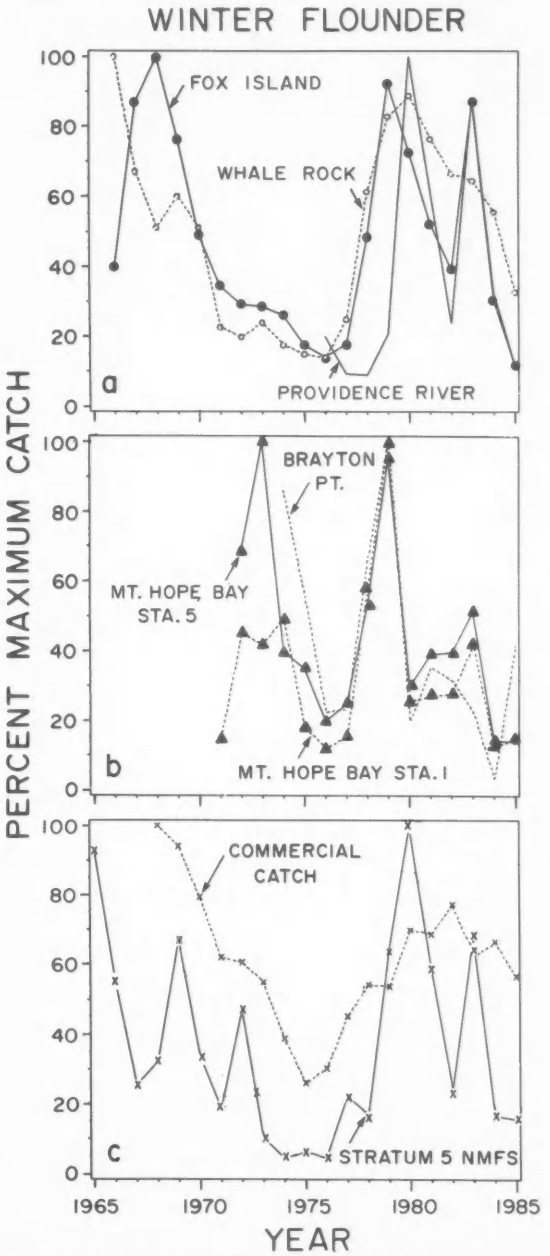

FIG. 8. Overlay plots of indices of yearly abundance (percent maximum catch) for regions which were significantly correlated ($P<0.10$), (a) Fox Island (●——●), Whale Rock (○- - -○), and Providence River (——), (b) Mt. Hope Bay; station 5 (▲——▲), station 1 (▲- - -▲) and Brayton Point (- - - -), and (c) National Marine Fisheries stratum 5 (×——×) and commercial catch (×- - - -×). Providence River and Brayton Point data were lagged by 1 yr.

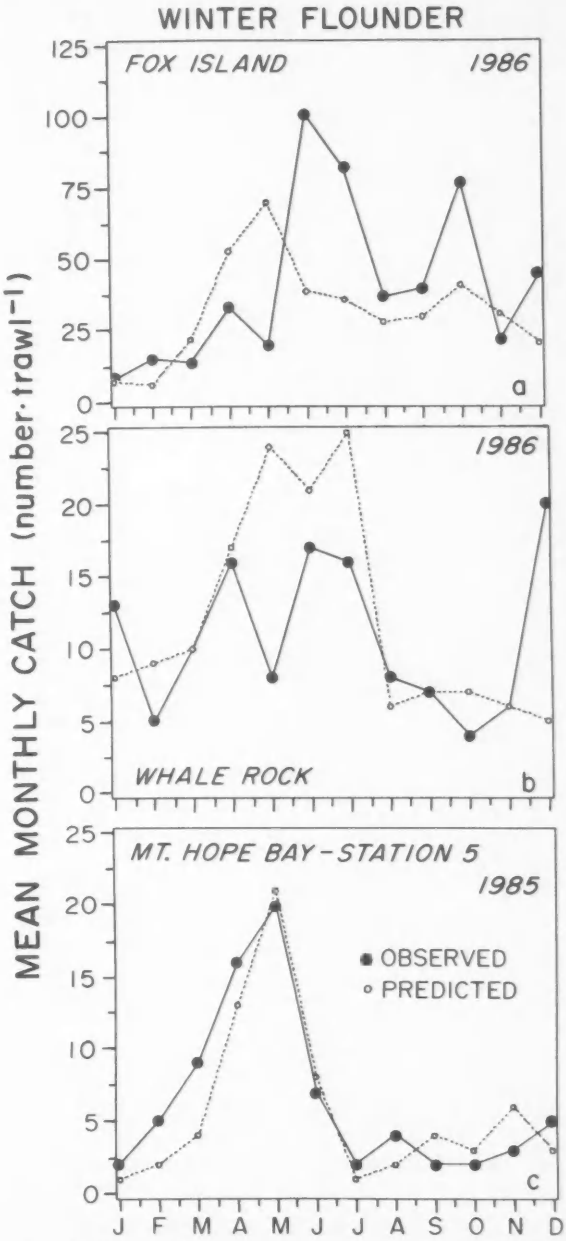

FIG. 9. Observed (solid line) and predicted (broken line) mean monthly catch for winter flounder at (a) Fox Island (number per 30-min trawl), (b) Whale Rock (number per 30-min. trawl), and (c) Mt. Hope Bay, station 5 (number per 15-min. trawl). (note different years).

error term. Interpretation of the model is consistent with the winter flounder's life history.

Applications of time-series analysis to monthly catch per tow (constant effort) or catch per unit effort are scarce. Mendelssohn (1981) described fluctuation in the monthly catch of skipjack tuna in Hawaii with a combined seasonal and regular ARIMA model. Tuna abundances are strongly seasonal; thus, seasonal differencing was required to induce stationarity. Unlike winter flounder, tuna did not show non-seasonal trends. Saila et al. (1980) described monthly fluctuations in lobster catch with a combined autoregressive moving average model. Mendelssohn and Cury (1987), using a multivariate time-series anal-

ysis that included sea-surface temperature, were able to explain 43% of the variation in biweekly catch per unit effort of small pelagic fish species off the Ivory Coast of Africa.

Time-series techniques have also been applied successfully to long-term, yearly catch per unit effort (Stocker and Hilborn 1981; Kirkley et al. 1982; Jensen 1985). For many trawl surveys, yearly data exist, but they are inadequate to accurately specify the structure of an appropriate ARIMA model. In such cases, Pennington (1985, 1986) has proposed an a priori model:

$$(4) \quad (1 - B)\, Z_t = (1 - \theta B)\, a_t.$$

Fogarty et al. (1986) used this model to filter measurement error from true (process) error in analyzing yearly catch for six species of fish in the Northwest Atlantic. The basic structure of their annual model is similar to the ARIMA model fitted above: the year-to-year behavior for the two models is the same. The data set we used, a 28-yr period of carefully standardized observation, was sufficiently complete to permit both prediction and comparison.

We also compared long-term patterns throughout the Narragansett Bay area. Correlation analyses showed that relative abundance was similar within the estuary and offshore. However, yearly abundance estimates in the Bay were not, in all cases, correlated with the offshore population (Table 4). Different investigators using different methods was not the reason, for there were several remarkably high correspondences among the individual programs.

Forecasting

The final ARIMA models (Table 2) explained 62–72% of the variation in the natural logarithm of flounder catch over 156–324-mo periods at the primary observation sites in Narragansett Bay. To make true monthly predictions (following Saila et al. 1980), we calculated the parameters from all but the last year's data, and then compared the models' prediction (untransformed) with the actual observed monthly catch (Fig. 9).

Peaks of spring migration out of the Bay, past successive observation points, were successfully predicted in Rhode Island Sound (Whale Rock) and in Mt. Hope Bay (Fig. 9). In the Bay's West Passage (Fox Island) the predicted peak occurred 1 mo before the observed peak for that year. It is not unusual to have a migration varying by a month from year to year. Generally, however, the amplitude and duration of seasonal fluctuations were accurately described. Cumulative monthly forecast errors, compared with observed annual indices of abundances, at Fox Island and Whale Rock were 21 and 11%, respectively; the error for Mt. Hope Bay was 12%. The observed values (Fig. 9) include the effects of sampling variability, which cannot be predicted, and thus forecasts may be even better than they appear.

The annual models predicted that winter flounder abundance at Fox Island and Whale Rock would recover in 1987 (Fig. 7): as of September, Bay catch had increased over the previous year, so it appears that the forecast was accurate.

We conclude that a long (>25 yr) time-series of relative abundance at a single observation point can predict the decline, as well as the recovery, of a most important demersal fish population. The ecological significance is that the time-series parameters are approximately the same for all of Narragansett Bay (Table 2). There appears to be an inherent uniformity of behavior, inshore and offshore, on which a single predictive model for winter flounder in the Northeast could be based.

This approach circumvents the often encountered problem in marine biology of noisy data and drifting due to random perturbation. Time-series analysis is useful for forecasting and confirming the time pattern in data. Processes may be the same in time and space even though localized changes in abundances look different. Southern New England's winter flounder population is a clear example.

Acknowledgements

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Density Dependence in Spiny Lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands

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A positive linear relationship between the ratio of natural mortality to von Bertalanffy growth and catch per unit effort (CPUE) and a negative relationship between asymptotic length and CPUE were observed for the spiny lobster, *Panulirus marginatus*, among seven banks in the Northwestern Hawaiian Islands prior to the development of a fishery (1977–81). Resampling two of these banks in 1986–87 after heavy fishing indicated an increase in the asymptotic length and a decrease in the length at onset of egg production.

Il existait une relation linéraire positive entre le ratio de la mortalité naturelle à la croissance von Bertalanffy et la prise par unité d'effort (PUE) ainsi qu'une relation négative entre la longueur asymptotique et la PUE chez la langouste, *Panulirus marginatus*, dans sept bancs de la partie nord-ouest de l'archipel hawaïen avant l'établissement d'une pêcherie (1977–81). Un nouvel échantillonnage de ces bancs en 1986–87, après une pêche intense, a indiqué un accroissement de la longueur asymptotique et une diminution de la longueur au moment de la production d'oeufs.

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Density-dependent relationships affecting growth, natural mortality, asymptotic size, and size at onset of sexual maturity in some lobster stocks have been difficult to rigorously document because of limitations in data bases and analytic methods (Chittleborough 1979; Morgan 1980; Munro 1983; Addison 1986). However, documenting these relationships is frequently cited as research critical to understanding lobster population dynamics (e.g. Cobb 1986). Addison (1986) hypothesized that, if a significant relationship between density and population parameters exists as a result of the lobster's use of shelters, management measures derived from changes in size-frequency distributions and standard yield-per-recruit models may be incorrect since they assume population parameters do not change with density.

Density-dependent relationships are examined for population parameters of the spiny lobster, *Panulirus marginatus*, in the Northwestern Hawaiian Islands (NWHI), a chain of small islands, banks, and reefs on the northwestern portion of the Hawaiian Archipelago (Fig. 1). Based on research sampling data from 1977 to 1981, estimates of density, in terms of catch per unit effort (CPUE); asymptotic length (L_∞); and the ratio of natural mortality to growth (M/K) for the spiny lobster are determined for seven NWHI banks prior to the development of a commercial fishery. Nine years after this initial sampling, an annual research program was initiated to resample the spiny lobster populations at Necker Island and Maro Reef, both having experienced heavy commercial fishing and reductions in lobster density. The changes in density, measured as changes in CPUE, are compared with changes in total mortality to growth (Z/K), L_∞, and size at onset of egg production.

Analytic Methods

Catch Rates

Standardized lobster sampling was conducted in 1977–81 at 26 banks in the NWHI and again in 1986–87 at Necker Island and Maro Reef, the two most productive and heavily fished banks. Lobster habitat at each bank was partitioned into 0.01 nmi^2 quadrats, and a randomly selected subset of the quadrats was fished at 20–90 m depths with California wire mesh, two-chambered lobster pots. The percent of the 0.01 nmi^2 quadrats sampled ranged from 60 to 90%; typically a greater proportion of the habitat was sampled at the smaller banks. At least eight strings of eight traps per string were baited and set overnight in each quadrat sampled. The trapped lobsters were measured and released at the trapping site. For each quadrat, the CPUE was computed as the number of lobsters trapped divided by the number of traps recovered. The bank CPUE and standard error were computed as the mean and standard error of the CPUE's from all the quadrats sampled.

The research sampling covered all seasons and at some banks extended for several years. However, neither seasonal factors nor trap selectivity appear to bias the trap data. Specifically, in a study on selectivity of traps as population sampling gear, MacDonald and Stimson (1980) compared lobster catch rates and size structure between trap and diver catches and observations at Kure Atoll in the NWHI. Their study concluded that (i) trap CPUE does not seem to be influenced by seasonal or lunar factors, (ii) trap catches do not appear to be influenced by a dominance hierarchy based on size, (iii) size distributions

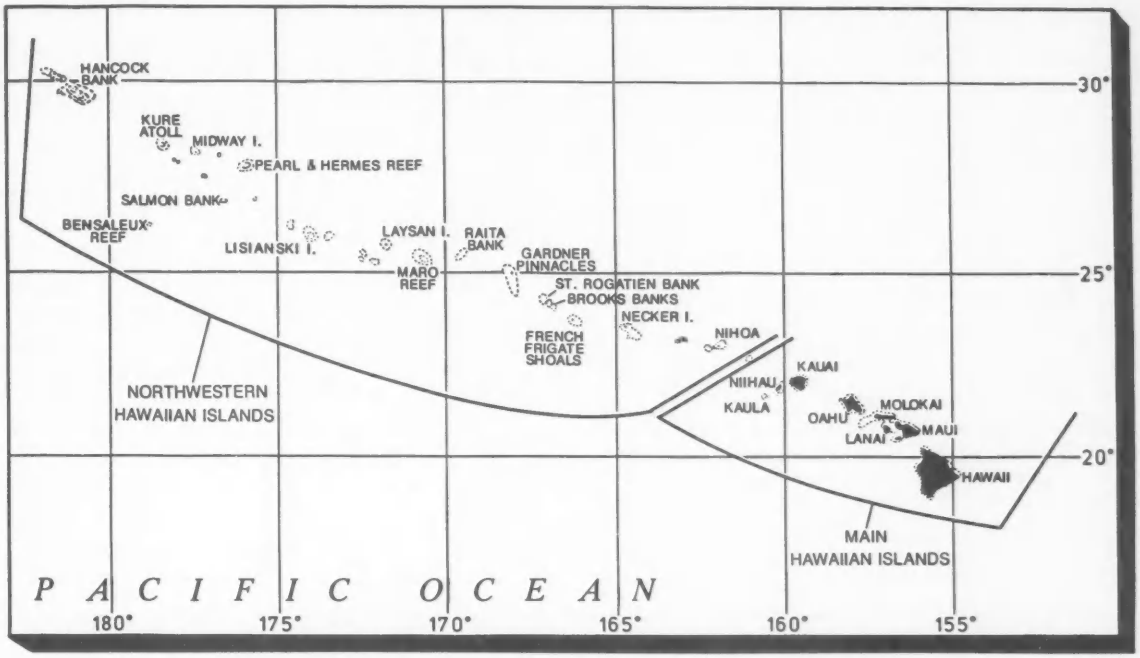

FIG. 1. The Hawaiian Archipelago, including the Northwestern Hawaiian Islands.

TABLE 1. Estimates of mean M/K, L_∞, and catch per unit effort (CPUE) (SE in parentheses) for lobster populations at seven banks in the Northwestern Hawaiian Islands. N denotes sample size.

Bank	Year	N	Mean CPUE	Mean L_∞	Mean M/K
Necker Island	1977	6474	5.76 (0.75)	113.8 (1.3)	4.22 (0.27)
Gardner Pinnacles	1977–80	390	1.68 (0.41)	115.0 (2.1)	2.20 (0.51)
Raita Bank	1977–80	384	1.13 (0.36)	128.1 (1.7)	1.56 (0.44)
Maro Reef	1977	2318	3.89 (0.45)	127.1 (1.9)	3.56 (0.30)
Laysan Island	1977	954	1.79 (0.39)	125.1 (2.5)	2.72 (0.49)
Pearl and Hermes Reef	1977–79	543	0.63 (0.20)	137.0 (2.2)	2.17 (0.39)
Midway	1977–79	896	1.48 (0.51)	117.2 (1.9)	2.55 (0.48)

of trap and diver-caught lobsters above about 85 mm carapace length show no difference, and (iv) trap CPUE appears to be a reliable measure of adult density.

Mortality to Growth Ratio and Asymptotic Length

Estimates of mortality and growth were computed as a ratio rather than separately because a recently developed estimator using length-frequency data permits estimates of this ratio that are more precise than if either parameter is determined separately (Wetherall et al. 1987). If growth and natural mortality vary with density, it will likely be a positive density and mortality relationship and an inverse density and growth relationship (Cobb and Phillips 1980). The ratio of mortality to growth is sensitive to both these relationships.

Although lobsters grow incrementally rather than continuously, the von Bertalanffy growth curve with parameters K and L_∞ adequately approximates a lobster growth curve (Morgan 1980). In the absence of fishing mortality under the assumptions of von Bertalanffy growth and a constant natural mortality rate (M) for lobsters above the smallest length fully represented in the catch (L_c), the length-frequency data can be used to estimate the ratio of instantaneous natural mortality to growth (M/K), with a relationship derived from the equation (Beverton and Holt 1957)

$$M/K = (L_\infty - \bar{l})/(\bar{l} - L_c),$$

where $\bar{l}$ is the mean length of all lobsters greater than L_c. Rearranging this equation to express $\bar{l}$ as a linear function of L_c gives

$$\bar{l} = L_\infty/((M/K) + 1) + L_c(M/K)/((M/K) + 1).$$

Now instead of treating L_c as a single value, a sequence of L_c and corresponding $\bar{l}$ values is constructed by beginning with the smallest L_c fully represented in the catch and increasing it in a regular fashion to the largest fish in the sample and computing an $\bar{l}$ for each. In practice, the lower limit of the first size class after the mode of the length-frequency distribution is used as the first L_c value, and each subsequent L_c value is taken as the lower limit of each progressively larger size class. Regressing the sequence of $\bar{l}$ values on the corresponding L_c values (weighted by the standard errors of $\bar{l}$) gives estimates of the slope and intercept of equation (1), which can be solved for L_∞ and M/K (Wetherall et al. 1987). When fishing mortality (F) is

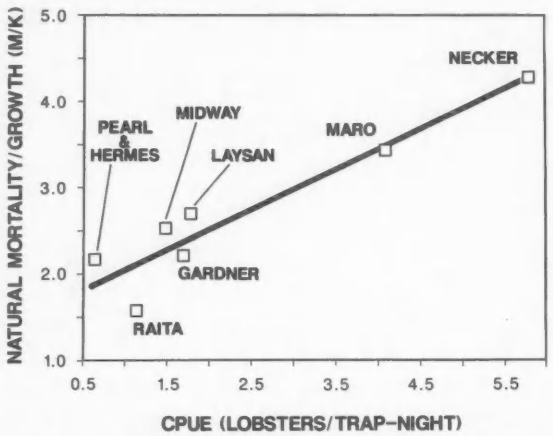

FIG. 2. Plot of the ratio of natural mortality to growth (M/K) against catch per unit effort (CPUE) for seven banks in the Northwestern Hawaiian Islands. The line is the regression equation $M/K = 1.63 + 0.46 \cdot \text{CPUE}$.

TABLE 2. Estimates of mean catch per unit effort (CPUE), Z/K, and L_∞ (SE in parentheses) for lobster populations at Necker Island and Maro Reef in 1986–87. N denotes sample size.

Location	N	Mean CPUE	Mean L_∞	Mean Z/K
Necker Island	2106	2.14 (1.24)	158.2 (5.3)	6.28 (0.57)
Maro Reef	2351	2.65 (0.67)	132.7 (0.63)	3.16 (0.10)

present, this method estimates the ratio of total mortality ($Z = M + F$) to growth (Z/K) and L_∞.

Because of differences in the length-frequency distributions between males and females, estimates of M/K and L_∞ were first computed for males and females separately, then averaged for a mean bank estimate.

Length at Onset of Egg Production

The research sampling recorded whether females were carrying external eggs. A function of the hyperbolic tangent (Tanh) is fit to the proportion of females with eggs (Y), where carapace length class (X) is the independent variable and parameters A, B, and C are estimated with the model

$$Y = A(1 + \text{Tanh}[B(X - C)]).$$

A weighted least squares estimation is used, where the weights are the number of females in the length class. The parameter C is the carapace length, where the percent of the females with eggs equals one-half the asymptotic level ($2A$), and this is taken as the estimate of length at onset of egg production (L_m).

Results

Although 26 banks were sampled in the NWHI for spiny lobsters (Uchida and Tagami 1984), only seven banks met the minimum sample size requirement based on a simulation analysis with the M/K and L_∞ estimation procedure (see Wetherall et al. 1987). Thus, the analyses used only the seven banks where size-frequency samples of at least 150 lobsters were measured for each sex, from a period prior to any significant fishing effort. Estimates of mean M/K, L_∞, and CPUE for each of the seven banks are in Table 1. A regression of mean bank M/K estimates on mean bank CPUE shows a significant positive relationship ($P<0.001$, $R^2 = 0.88$; Fig. 2). Lobsters at banks with high CPUE have significantly higher natural mortality or lower growth or both than at banks with low CPUE.

A regression of L_∞ on mean CPUE suggests that these variables are negatively correlated, but the result is not statistically significant ($P = 0.27$). However, simulation studies show that the estimates of L_∞ can be negatively biased for small sample sizes (Wetherall et al. 1987). When L_∞ is regressed on CPUE with a weighted regression where the weights correspond to the sample size of lobsters measured at each bank, the coefficient of CPUE is estimated as -2.6, which is statistically significant ($P = 0.08$) and indicates L_∞ varies inversely with CPUE.

Necker Island and Maro Reef experienced considerable fishing effort after 1980; the greatest decline in CPUE occurred at Necker Island, which is closer to the fishing port in Honolulu and has a smaller area of productive habitat than Maro Reef. The 1986–87 mean CPUE's were 37 and 68% of their 1977 levels at Necker Island and Maro Reef, respectively (Table 1, 2). At Necker Island, the mean L_∞ was estimated at 158.2 mm for 1986–87 and at 113.8 mm prior to the fishery. The difference in L_∞ between the two periods is statistically significant ($P<0.05$) (Table 1, 2; Fig. 3). At Maro Reef, even though initially L_∞ was relatively large there was a statistically significant increase in L_∞, although much less than that observed at Necker Island, after the reduction in CPUE ($P<0.05$) (Table 1, 2).

Although estimates of M/K are unavailable for Maro Reef and Necker Island for 1986–87, estimates of M/K for 1977 compared with estimates of Z/K for 1986–87 strongly suggest that M/K declined at both banks as CPUE declined. At Maro Reef, M/K for 1977 and Z/K for 1986–87 did not significantly differ. Because the 1986–87 CPUE is 68% of the 1977 level, fishing mortality must be substantial, and hence, M/K must have declined in 1986–87. At Necker Island, Z/K is greater than the 1977 M/K; however, if F/M is estimated as the difference between the 1986–87 Z/K and 1977 M/K divided by the 1977 M/K, an F/M estimate of 0.49 is obtained. This estimate very likely underestimates the ratio of fishing mortality to natural mortality, given that 1986–87 CPUE is 37% of the 1977 level.

Using the Beverton and Holt (1957) yield equation to estimate the reduction in population biomass of a stock relative to its unexploited level as a function of F/M (Beddington and Cooke 1983), when $M/K = 3$, the exploitable biomass will be reduced to 55 and 37% of the level prior to exploitation when $F/M = 0.5$ and 1.2, respectively. Thus, at Necker Island, the reduction of the 1986–87 CPUE to 37% of the unexploited level suggests F/M exceeded 1.0 and certainly the 0.49 estimated under the assumption that M/K is density independent. If F/M were 0.50, the 1986–87 CPUE would be expected to be about 50% of the 1977 level. The M/K, which corresponds to the 1986–87 CPUE level of 2.14, can be calculated from the equation derived from the regression of M/K on CPUE for the seven banks (Fig. 2). This equation estimates $M/K = 2.73$ at Necker Island in 1986–87. With this estimate of M/K and Z/K of 6.28, F/M is estimated to be 1.3, which is consistent with the estimate from the Beverton and Holt (1957) equation given the level at 1986–87 CPUE relative to 1977.

The percentage of females sampled with external eggs increased as a function of carapace length from zero to an asymptotic level (Fig. 4). By 1987, carapace lengths at onset of egg production at both Necker Island and Maro Reef were

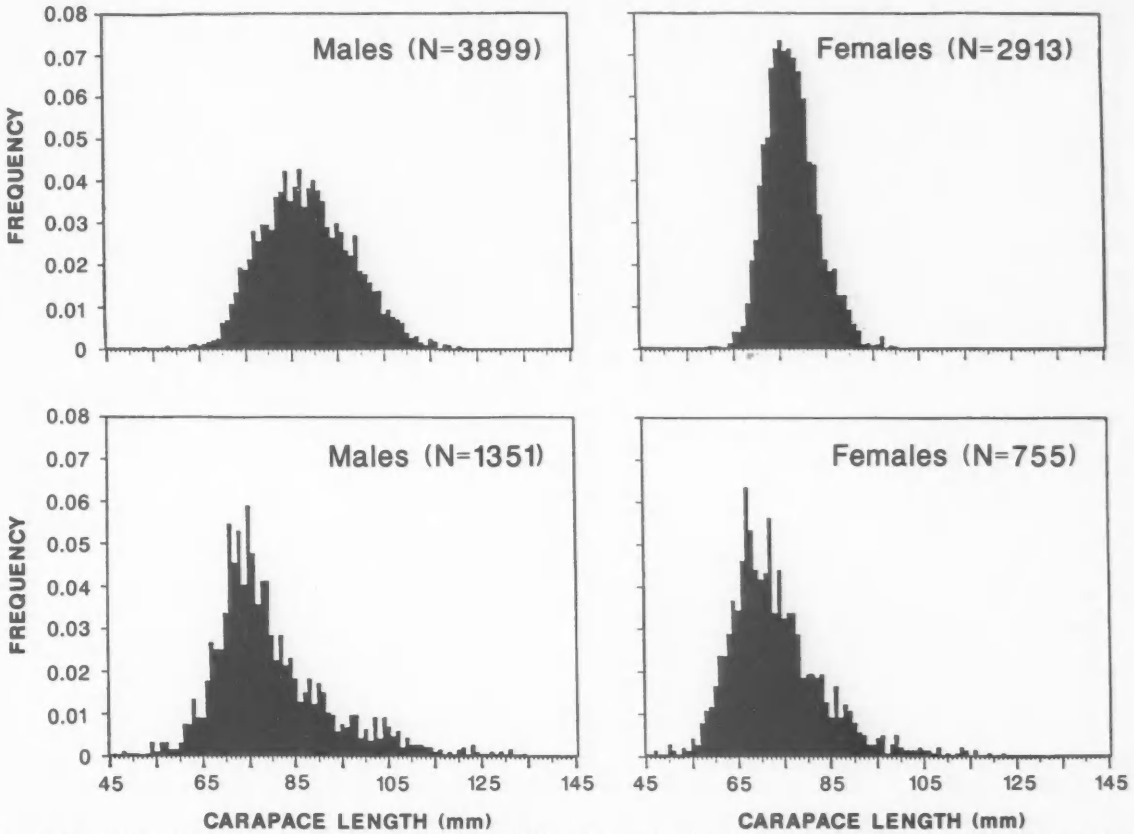

FIG. 3. Plots of length-frequency samples for male and female lobsters from Necker Island obtained from 1977 (top) and 1986–87 (below) sampling periods. (*N* denotes the number of lobsters in each sample.)

significantly lower than in 1977 ($P<0.05$) (Table 3). At Necker Island, the length declined from 67.8 mm in 1977 to 60.8 mm in 1987 (Table 3). At Maro Reef, the length declined from 74.8 mm in 1977 to 68.2 mm in 1987 (Table 3).

Discussion

A positive relationship has been shown to exist between *M*/*K* and CPUE over seven banks. The similarity in coral reef habitat and reef fauna between these banks (Grigg 1984; Hobson 1984), the evidence that trap catches are a reliable measure of adult abundance and size structure (MacDonald and Stimson 1980), and the indication that *M*/*K* decreases with CPUE at Necker Island and Maro Reef when density is reduced due to fishing — all argue that this relationship is likely not due to other factors, which might differ between banks, and further indicate a positive relationship between *M*/*K* and density. As to whether the change in the ratio of *M* to *K* is due to changes in *M* or changes in *K* or both, the separate estimates of the parameters needed to address that issue are not available. However, studies on other species of spiny lobsters suggest that it is likely that both *M* and *K* change with density. Munro (1983) estimated the natural mortality coefficient (*M*) for *P. argus* was 0.52 for an unexploited stock, 0.23 for a moderately exploited stock, and 0.14 for a heavily exploited stock. A similar relationship between density and natural mortality was indicated in *P. cygnus* (Cobb and Phillips 1980). Likewise, growth can be influenced by food and space availability, which change as density changes (Cobb and Phillips 1980).

The inverse relationship between L_∞ and CPUE, both between banks and over time at Necker Island and Maro Reef, is consistent with the hypothesis that asymptotic size changes inversely with density. Differences in the volume of shelters at two areas in England have been suggested as the cause of marked differences in the size structure of the lobster, *Homarus gammarus*, populations: the area where large shelters are abundant also has more large lobsters (Howard 1980). In the NWHI, the banks all have the same coral reef habitat, so it is unlikely that the size structure of the habitat differs between banks. However, when density is high, crowding may occur even in large shelters and effectively reduce shelter size.

Changes in the length at onset of maturity apparently due to changes in density have been observed in some fish populations. Shelton and Armstrong (1983) documented a 3-cm decline in the length at maturity of the South African pilchard, *Sardinops ocellata*, during a period of substantial population decline. By contrast, there was a 1-cm increase in the length at onset of sexual maturity in the South African anchovy, *Engraulis capensis*, after a period of population increase. Rothschild (1986) suggested that, when a population experiences a reduction in density, the increase in available food for each individual will result in an increase in the rate of sexual development and

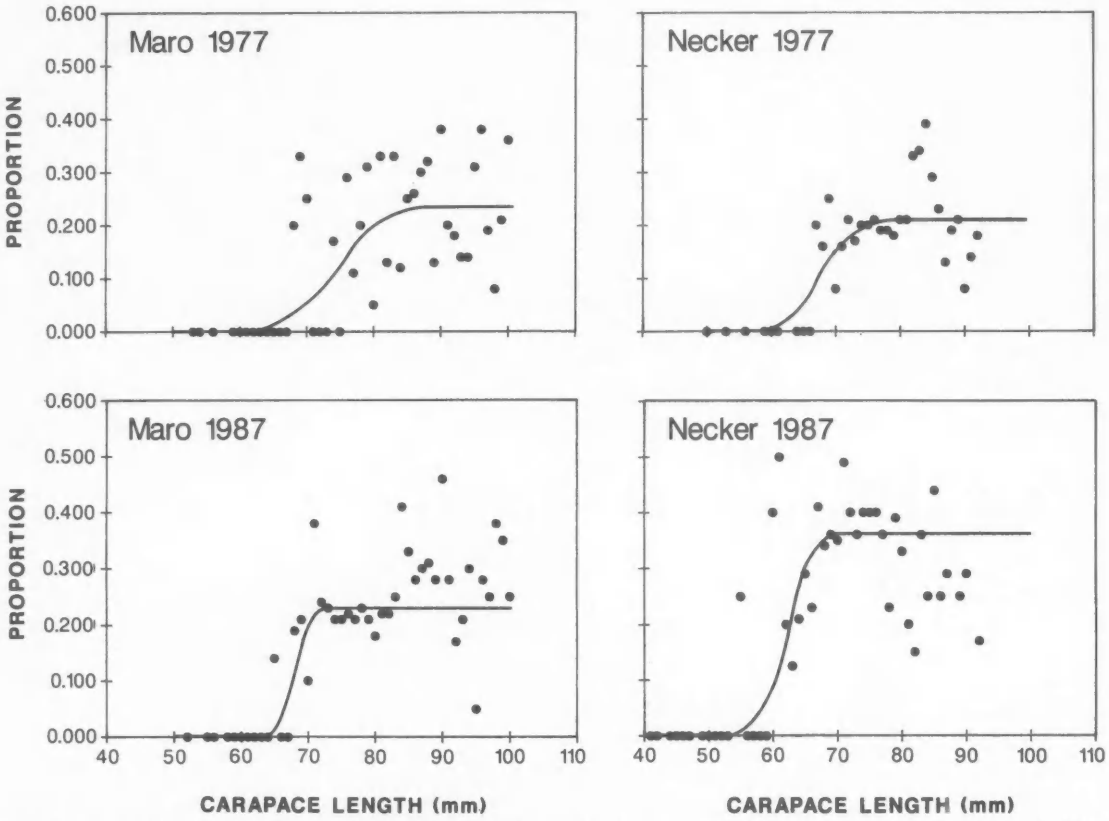

FIG. 4. Proportion of female spiny lobsters at Necker Island and Maro Reef with eggs as a function of carapace length for 1977 and 1987.

TABLE 3. Length at onset of egg production for 1977, 1985–86, and 1987. CL = carapace length (mm) (SE in parentheses), L_m/L_∞ = ratio of length at onset of egg production to female asymptotic length, and N denotes sample size.

	1977			1985–86			1987		
Location	N	CL	L_m/L_∞	N	CL	L_m/L_∞	N	CL	L_m/L_∞
Necker Island	1955	67.8 (1.5)	0.66	1491	57.9 (1.0)	0.41	797	60.8 (1.1)	0.47
Maro Reef	630	74.8 (2.5)	0.61	1614	70.5 (1.9)	0.59	873	68.2 (0.8)	0.54

hence an attainment of the onset of sexual maturity at a smaller size. However, it is also possible that behavioral interactions are important and smaller females are responding not just to a reduction in density but also to a reduction in number of larger females. The observed reductions in length of egg-bearing females at Necker Island and Maro Reef are consistent with both these hypotheses.

A hypothesis that the size at onset of egg production is determined exclusively by age has been used to explain differences in the size at onset of egg production for the rock lobster, *Jasus lalandii*, in different areas of the Benguela ecosystem (Beyers and Goosen 1987). It is argued that the differences in the size at onset of egg production result from differences in growth, so faster growing lobsters are larger when they reach the age at onset of sexual maturity. If the onset of egg production is determined exclusively by age and if growth increases when density is reduced by fishing, then the size at the onset of egg production should increase as fishing increases and not decrease as observed in the NWHI. An explanation for the difference between this hypothesis and the NWHI findings is that the NWHI fishery only harvests lobsters above the size at onset of egg production; hence, there is no reduction in juvenile lobsters and perhaps no increase in juvenile lobster growth, even though total lobster density decreases.

A management implication of the finding that M/K and L_∞ vary with density is that the application of static yield-per-recruit models can be misleading. Suppose managers want to determine the minimum length at which spiny lobsters should be harvested to maximize the yield-per-recruit at Necker Island when F/M is at 1.3 (estimated 1986–87 level). The Beverton and Holt (1957) yield-per-recruit model can be formulated in terms of M/K, Lr/L_∞, and F/M, where Lr is the length at entry to the fishery (Beverton and Holt 1966). If this model is used with the 1977 data ($M/K = 4.22$; $L_\infty = 114$ mm), the minimum length to maximize yield-per-recruit will be set at 41 mm. However, based on the estimated values of M/K and L_∞ (M/K

estimated from the M/K versus CPUE regression) in 1986–87, the minimum length should be 67 mm. The fishery operating with a minimum length of 41 mm will have a yield-per-recruit that is 20% lower than the maximum achieved with the 67 mm minimum length under the 1986–87 population parameters.

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Feeding Flexibility in Northern Pike (*Esox lucius*): Fish versus Invertebrate Prey

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Chapman, L. J., W. C. Mackay, and C. W. Wilkinson. 1989. Feeding flexibility in northern pike (*Esox lucius*): fish versus invertebrate prey. Can. J. Fish. Aquat. Sci. 46: 666–669.

We describe the frequency of occurrence of fish and invertebrates in the stomach contents of northern pike (*Esox lucius*) from eight populations in Alberta and the Northwest Territories. Lakes were sampled one to eight times between 1979 and 1985, and a total of 899 pike were examined (mean standard length = 44 ± 8 cm, SD). Although northern pike are widely considered to be top aquatic piscivores, we found that the frequency of occurrence of invertebrates was high, at least on a seasonal basis, in some systems. In all of the lakes considered, the frequency of occurrence of fish (expressed as a percentage of non-empty stomachs) was 88% or greater in one or more of the sample periods. However, diets where the frequency of occurrence of invertebrates was greater than 90% occurred in three of the populations in one or more of the sample periods. The frequency of occurrence of invertebrates was negatively correlated with the percentage of empty stomachs, while the frequency of occurrence of fish was positively related to the percentage of empty stomachs. Invertebrate feeding was not limited exclusively to smaller pike; invertebrates were found in the stomachs of pike 24 to 60 cm long (standard length).

Les auteurs décrivent la fréquence d'occurrencce de poissons et d'invertébrés dans l'estomac du grand brochet (*Esox lucius*) chez huit populations d'Alberta et des Territoires du Nord-Ouest. Au total, 899 brochets ont été examinés (longueur type moyenne = 44 cm ± 8 cm d'écart type) dans des lacs échantillonnés une à huit fois entre 1979 et 1985. Bien que le grand brochet soit généralement considéré comme étant un piscivore qui se nourrit d'animaux occupant le haut de la chaîne alimentaire aquatique, les auteurs ont trouvé que la fréquence d'occurrence d'invertébrés était élevée, au moins sur une base saisonnière, dans certains systèmes. Dans tous les lacs échantillonnés, la fréquence d'occurrence de poissons (exprimée sous forme de pourcentage des estomacs non vides) était supérieure ou égale à 88 % au cours d'une ou plusieurs périodes d'échantillonnage. Cependant, une fréquence d'occurrence d'invertébrés supérieure à 90 % s'est manifestée dans trois des populations au cours d'une ou plusieurs périodes d'échantillonnage. La fréquence d'occurrence d'invertébrés présentait une corrélation négative avec le pourcentage des estomacs vide, tandis que la fréquence d'occurrence de poissons était corrélée de façon positive avec le pourcentage des estomacs vides. Ce ne sont pas seulement les plus petits brochets qui se nourrissent d'invertébrés puisque des invertébrés ont été découverts dans des estomacs de brochets atteignant 24 et même 60 cm de longueur (longueur type).

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The body morphology of the pike (*Esox lucius*) would appear to be fine-tuned towards a piscivorous feeding mode. Its broad, flattened snout, large mouth, large teeth, and heavy jaws are all adapted for a vertebrate-oriented diet (Keast and Webb 1966; Bucke 1971). In addition, the short esophagus, large pouch like stomach, and relatively short intestine are related to a piscivorous diet (Bucke 1971). Although young pike (less than 50 mm) have been reported to feed primarily on entomostracans and insects (Hunt and Carbine 1951; Frost 1954), larger pike have generally been reported to be strongly piscivorous (Frost 1954; Seaburg and Moyle 1964; Lawler 1965; Wolfert and Miller 1978; Diana 1979; Bregazzi and Kennedy 1980). Considering the broad circumpolar distribution of northern pike in the Northern hemisphere (McPhail and Lindsey 1970), one might expect pike to be a highly flexible species differing from lake to lake in many parameters, including diet.

In this study, we describe the stomach contents of northern pike from nine lakes in Alberta and the Northwest Territories with respect to the frequency of occurrence of invertebrate and vertebrate prey. Although northern pike are generally considered piscivorous in nature, we demonstrate that the frequency of occurrence of invertebrate prey in their diet is high on occasion in some systems.

Methods

As part of a larger study, northern pike were collected using gill nets (generally set overnight) from nine lakes in Alberta and the Northwest Territories (Table 1). Populations were sampled one to eight times during open water periods from 1979 to 1985. A total of 899 pike with a mean standard length of 44 ± 8 cm, SD (range = 22–101 cm) and a mean weight of 883 ± 659 g, SD (range = 98–8675 g) were examined.

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TABLE 1. Location of lakes, mean standard length, and frequency of occurrence of invertebrates and vertebrates in the stomachs of northern pike collected from nine North American lakes.

Lake	Location	Total number collected	Mean length (cm ± SD)	Date	Frequency of occurrence of invertebrates (percent)	Frequency of occurrence of vertebrates (percent)	Number of empty stomachs (percent)	Number of non-empty stomachs (percent)
Lac Ste. Anne, Alberta	114°24′W 53°43′N	176	44 ± 6 range, 22–60	May 1982	0 (0)	8 (100)	18 (69)	8 (31)
				June 1982	4 (36)	7 (64)	6 (35)	11 (65)
				July 1982	1 (14)	6 (86)	13 (65)	7 (35)
				Sept. 1982	0 (0)	4 (100)	5 (56)	4 (44)
				June 1983	1 (20)	4 (80)	9 (64)	5 (36)
				July 1983	2 (6)	29 (94)	22 (42)	31 (58)
				Aug. 1983	3 (38)	7 (88)	8 (50)	8 (50)
				Sept. 1983	1 (10)	10 (100)	11 (52)	10 (48)
Tucker Lake, Alberta	110°37′W 54°32′N	256	45 ± 5 range, 32–58	June 1979	37 (100)	5 (14)	1 (3)	37 (97)
				Aug. 1979	1 (9)	11 (100)	29 (73)	11 (28)
				May 1980	16 (94)	2 (12)	4 (19)	17 (81)
				June 1980	15 (100)	0 (0)	9 (38)	15 (63)
				July 1980	1 (6)	16 (100)	44 (73)	16 (27)
				Aug. 1980	0 (0)	14 (100)	4 (22)	14 (78)
				Sept. 1980	0 (0)	9 (100)	15 (63)	9 (38)
				June 1982	20 (100)	0 (0)	11 (35)	20 (65)
Narrow Lake, Alberta	113°37′W 54°35′N	62	40 ± 7 range, 22–60	May 1983	14 (100)	9 (64)	3 (18)	14 (82)
				June 1983	1 (50)	1 (50)	3 (60)	2 (40)
				July 1983	3 (43)	5 (71)	1 (13)	7 (88)
				Aug. 1983	7 (78)	7 (78)	4 (31)	9 (69)
				Sept. 1983	0 (0)	4 (100)	15 (79)	4 (21)
Kakisa Lake, NWT	117°43′W 60°56′N	69	51 ± 12 range, 34–87	July 1979	0 (0)	1 (100)	8 (89)	1 (11)
				Aug. 1979	0 (0)	15 (100)	25 (63)	15 (38)
				Aug. 1980	0 (0)	8 (100)	12 (60)	8 (40)
Campbell Lake, NWT	133°50′W 68°15′N	135	45 ± 12 range, 29–101	July 1982	6 (24)	21 (84)	23 (48)	25 (52)
				Sept. 1984	0 (0)	6 (100)	21 (78)	6 (22)
				June 1985	8 (24)	31 (91)	26 (43)	34 (57)
Shell Lake, NWT	133°37′W 68°18′N	73	36 ± 5 range, 30–51	July 1982	23 (100)	4 (17)	1 (4)	23 (96)
				June 1985	22 (55)	36 (90)	9 (18)	40 (82)
Inuvik Lake, NWT	133°51′W 68°18′N	50	48 ± 7 range, 32–76	July 1982	6 (23)	23 (88)	24 (48)	26 (52)
East Round/ Bonnetplume Lakes, NWT	133°53′W 68°40′N	78	46 ± 8 range, 28–82	Aug.–Sept. 1984	0 (0)	12 (100)	22 (65)	12 (35)
				June 1985	13 (41)	29 (91)	12 (27)	32 (73)

Fish were killed, weighed, and standard length was measured. Stomach contents were examined, and individual prey items or parts thereof were removed. The frequency of occurrence of major prey types (fish, invertebrates) was determined for each lake in each sample period. The frequency of occurrence was calculated as the percentage of non-empty stomachs containing a particular prey type. This method does not consider the amount or bulk of food types per stomach; however, it is a quick and efficient method of providing a crude assessment of the diet spectrum (Hyslop 1980). Data from East Round and Bonnetplume Lakes were pooled as one population because the two lakes were separated by a short (approximately 250 m long) stream in which pike were observed moving, and the lakes were similar in basin morphometry and fauna.

Results

In all of the lakes considered, the frequency of occurrence of fish was 88% or greater in one or more of the sample periods (Table 1). In six of the eight populations examined, one or more of the sample periods reflected an entirely piscivorous diet (frequency of invertebrates = 0%). Of the fish that were identified, coregonids (*Coregonus* sp.), nine-spined stickleback (*Pungitius pungitius*), and smelt (Osmeridae) were the major fish prey consumed by populations sampled in the Northwest Territories. Yellow perch (*Perca flavescens*) were the dominant vertebrate prey in the southern lakes. Yellow perch were not found in lakes sampled north of 60°N, while they were present in all of the southern lakes. Diets where the frequency of occurrence of invertebrates was 94% or greater occurred in three of the lakes, in one or more of the sample periods (Shell Lake, July 1982; Narrow Lake, May 1983; and Tucker Lake, June 1979, May–June 1980, June 1982). In Shell Lake and Tucker Lake, the frequency of occurrency of fish was low (≤17%) during those sample periods when the frequency of occurrence of invertebrates was 94% or greater. In Tucker Lake, where data were collected on eight occasions, the pike population exhibited a

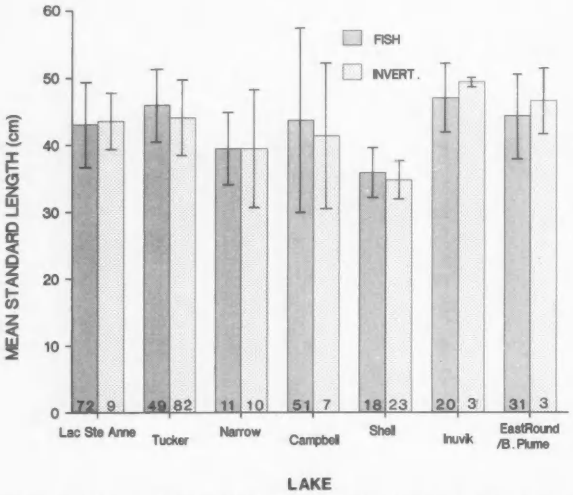

FIG. 1. Mean standard length (±SD) of pike with only fish in their stomachs and pike with only invertebrates in their stomachs for each of seven populations sampled in Alberta and the Northwest Territories (all sample periods pooled for a given lake). Fish with both invertebrates and fish in their stomachs are not included in this analysis. The frequency of occurrence of invertebrates in Kakisa Lake was 0%. Sample size is indicated at the base of each bar.

pronounced seasonal dietary shift. In this lake, there was a decrease in the frequency of occurrence of invertebrates in the stomachs from 94% or greater in May and June of 1980 to 6% or less in July, August, and September of the same year. There was a corresponding increase in the frequency of occurrence of vertebrates from 12% or less in May and June to 100% in July, August, and September (Table 1). This trend is supported by periodic samples in other years in Tucker Lake. In general, amphipods were the major invertebrate prey consumed, with the exception of Narrow Lake, where odonatans and ephemeropterans were frequently found in the stomachs of pike.

There was a negative relationship between the percent frequency of occurrence of invertebrates in the diet and the percentage of empty stomachs (Spearman's coefficient of rank correlation: rho $= -0.754$, $P<0.001$, $n = 32$). Correspondingly, there was a positive relationship between the percent frequency of occurrence of fish in the diet and the percentage of empty stomachs (Spearman's coefficient of rank correlation: rho $= 0.672$, $P<0.001$, $n = 32$).

An obvious consideration is the idea that invertebrate-feeding may be limited to smaller pike. However, Fig. 1 demonstrates that reasonably large pike fed on invertebrates. Among the lakes considered, there was no significant difference between the mean standard length of pike with only invertebrates in their stomachs and the mean standard length of pike with only fish in their stomachs (Wilcoxon Matched-Pairs Test, $P = 0.80$, $n = 7$, Fig. 1). Overall, the mean standard length of pike with only invertebrates in their stomachs was 42 cm (±7 cm, SD), the mean standard length of pike with fish and invertebrates in their stomachs was 41 cm (±7 cm, SD), and the mean standard length of pike with only fish in their stomachs was 44 cm (±9 cm, SD). This suggests that invertebrate feeding was not necessarily exclusive to the smallest fish collected (standard length). Over the nine lakes considered, invertebrates were found in the stomachs of pike which ranged in size between 24 and 60 cm (standard length). Fish were found in the stomachs of pike which ranged in size between 22 and 101 cm (standard length). It is possible that very large pike (≥ 60 cm) may be less likely to consume invertebrate prey. However, we examined very few pike ($n = 11$) 60 cm or greater in length that contained food in their stomachs, so we cannot clearly evaluate this idea.

Discussion

The morphological and behavioural characteristics of northern pike are typical of piscivorous fishes. However, we have demonstrated that pike are not necessarily piscivorous. The frequency of occurrence of invertebrates was high on occasion in three of the eight populations. Invertebrate feeding was not exclusive to small pike; both large and small pike ate invertebrates. Although many previous studies which have examined the food habits of northern pike have documented primarily piscivorous diets, invertebrate feeding has been reported in other studies (e.g. Solman 1945; Munro 1957). It should be noted that the use of frequency of occurrence methods to characterize diets can potentially overemphasize the importance of small prey items in the diet. Future studies in this area should address the relative importance of invertebrate and vertebrate prey by considering the number and weight or volume of different prey types in the stomachs and/or the relative energetic importance. Clearly, though, our results indicate that pike are flexible with respect to dietary characteristics. The observed variation in diet suggests that the feeding strategies of pike may be greatly modified in response to the availability of different prey types.

We found a positive relationship between the percentage of empty stomachs and the frequency of occurrence of fish in the stomachs of the pike. In many piscivorous pike populations empty stomachs are common (e.g. Frost 1954; Seaburg and Moyle 1964; Nursall 1973; Diana 1979), suggesting that pike are asynchronous feeders and that the time between their meals exceeds digestion time (Diana 1979). We found a negative relationship between the percentage of empty stomachs and the frequency of occurrence of invertebrates in the diet. A number of studies have demonstrated that large chitinous pieces from invertebrates may linger in the stomach longer than associated digestible organic matter (Windell 1966; Kionka and Windell 1972). This may account to some degree for the negative relationship observed. It also seems reasonable to suggest that when a pike is feeding primarily on relatively small organisms such as amphipods, a large number of small items must be captured and consumed to meet the energy requirements of the fish. Thus, there may be a higher feeding frequency and less time for the stomach to be empty. Allen (1935) found that in yellow perch, a shift to larger prey in larger perch from smaller prey in smaller fish, was accompanied by an increase in the percentage of empty stomachs. In laboratory studies of prey capture, growth rate, and ration size in pike, Hart and Connellan (1984), found that pike consumed a decreasing number of prey (minnows) with increasing prey size, and consequently spent less time feeding during the day.

Northern pike have a broad circumpolar distribution and are found in a wide variety of habitat types. Thus, one might expect the pike to be an ecologically flexible species with respect to diet. In addition the seasonally dynamic nature of temperate lakes may favour flexibility in resource use. Our data demon-

strate that pike are potentially capable of feeding on both vertebrate and invertebrate prey.

Liem (1984) presents and reviews evidence suggesting that there is a great deal of functional versatility in the prey capture mechanism of teleost fishes and a plasticity related to the aquatic medium which facilitates extraordinary potential for feeding flexibility. Our study provides evidence to support the idea of functional versatility in the feeding of one teleost fish species. Certainly, we must not ignore the functional constraints of body morphology, but should perhaps, reexamine the potential for flexibility in the feeding strategies of teleost fishes, such as the northern pike.

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Optimal Environmental Window and Pelagic Fish Recruitment Success in Upwelling Areas[1]

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Food availability and physical constraints such as turbulence are now considered as important factors that affect larval survival and pelagic fish recruitment. In Ekman-type upwelling, vertical advection, new inputs of nutrients and turbulence are linked to wind speed. According to the literature, food availability for larvae is related to biological dynamics (primary production) up to a point where the biological processes are disturbed by physical processes (turbulence generated by wind mixing). This limitation does not exist for non Ekman-type upwelling where upwelling intensity is not correlated with wind speed. We hypothesize that relations between annual recruitments and upwelling intensity are dome shaped in Ekman-type upwellings and linear for non Ekman-type upwellings. A statistical method is used to analyse the form of the relationships between recruitments and upwelling indices or wind mixing. The recruitment of the Peruvian anchoveta (*Engraulis ringens*), of the Pacific sardine (*Sardinops sagax caerulea*) and of the West African sardines and sardinellas are thereby examined. Results show that for Ekman-type upwelling the annual recruitment increases with upwelling intensity until wind speed reaches a value of roughly 5–6 $m \cdot s^{-1}$ and decreases for higher values. For a non Ekman-type upwelling the relationship between recruitment and upwelling intensity is linear. These results confirm the existence of an optimal environmental window for recruitment.

La disponibilité en nourriture et des contraintes physiques comme la turbulence sont des facteurs importants pour la survie des larves et le recrutement des espèces pélagiques. Dans un upwelling d'Ekman, les mouvements verticaux, les apports en sels minéraux et la turbulence sont liés à la vitesse du vent. D'après la littérature, la disponibilité en nourriture pour les larves est associée à des processus biologiques (production primaire) qui peuvent être perturbés par des processus physiques (turbulence). Ce facteur limitant disparait quand l'intensité de l'upwelling est indépendante du vent local. Nous proposons une relation en forme de dôme entre le recrutement et l'intensité de l'upwelling pour un upwelling d'Ekman et linéaire pour les autres types d'upwellings. Une méthode statistique est utilisée pour analyser la forme des relations entre recrutement, les indices d'upwelling ou la turbulence. Le recrutement de l'anchois du Pérou (*Engraulis ringens*) de la sardine du Pacifique (*Sardinops sagax caerulea*) et des sardines et sardinelles ouest-africaines est étudié. Les résultats montrent que, dans les upwellings d'Ekman, le recrutement annuel s'accroît avec l'intensité des upwellings jusqu'à ce que le vent atteigne une vitesse proche de 5–6 $m \cdot s^{-1}$ et décroît ensuite pour des vitesses plus élevées. Quand l'intensité des upwellings est indépendante des vents locaux et que la turbulence est faible, la relation entre recrutement et upwelling est linéaire. Ces résultats confirment l'existence d'une fenêtre environnementale optimale pour le recrutement.

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Large variability in pelagic fish recruitment is frequent and may have an important effect on fisheries (Smith 1985). Larvae survival is especially variable and the role of different sources of mortality at the prerecruit stage has been intensively studied. The main causes of larval mortality appear to be starvation and predation (Blaxter and Hunter 1982) and several environmental factors have a determinant effect on recruitment (Shepherd et al. 1984). Currently two theories have emerged to explain recruitment success in relation to environment. With the match–mismatch hypothesis, Cushing (1975) emphasizes that the annual production of fish larvae is matched or mismatched to the production of their food. In other words, a stock releases its larvae into the annual production cycle at the best time to secure good survival on average. The importance of food availability for larvae is the core of this energetic approach. The second hypothesis is based on Hjort's (1914, 1926) suggestion; early first feeding for larvae is the most vulnerable stage in the life history of fish. Some authors (Lasker 1975, 1981a, 1985; Peterman and Bradford 1987) provide evidence that turbulence in the euphotic layer increases larval mortality during "critical periods" (May 1974). A stable environment is usually needed to allow aggregations of food organisms to be formed and maintained. This stability hypothesis (Lasker 1981b) takes into account dynamic physical processes even though food availability is again the crucial factor for larval survival.

The time and space scales used for these studies are mostly microscales (Lasker 1978; Methot 1983; Peterman and Bradford 1987). It is interesting to try to reconcile the ideas which have been developed within a fine scale using a broader scale. In this paper we analyze the relationships that may exist between

[1]This work is dedicated to Dr. Reuben Lasker, a generous man and a pioneer in recruitment studies.

annual recruitment indices and upwelling intensity or wind mixing for some pelagic fish stocks in upwelling areas. The comparison between areas where upwelling intensity and wind mixing are closely related and areas where they are independent will illustrate the potential effect of turbulence on recruitment.

Analysis of the Relationships between Recruitment and Upwelling

Upwelling and Turbulence in Pelagic Fish Habitats.

The main coastal upwelling areas are located on the eastern boundaries of the oceans where the equatorward trade winds induce offshore Ekman transport. Cold, nutrient rich subsurface waters are brought to the euphotic layers enhancing primary production. Weak winds reduce primary productivity because they disrupt the upwelling process and the renewal of nutrients in the surface layers (Huntsman and Barber 1977). In the classical Ekman scheme the magnitude of the offshore transport in the upper layer is considered to be an indication of the amount of water upwelled along the coast into the surface layers (Bakun 1973). Higher wind induces higher offshore transport and increases upwelling. Therefore upwelling intensity and nutrient input into the euphotic layers could be estimated using offshore Ekman transport calculated from the wind component parallel to the coast. Ekman-type upwellings are found off Peru, California, Morocco, and Senegal.

Off Ivory Coast and Ghana, trade winds are weak and the strong cooling of the sea surface temperature during the boreal summer cannot be interpreted as classical Ekman-type upwelling (Bakun 1978; Picaut 1983). All attempts to correlate the intensity and duration of this upwelling with local winds have failed (Houghton 1976). Many mechanisms have been proposed as explanations of this upwelling among which are internal waves generated in the western part of the Atlantic (O'Brien et al. 1978), upward thermocline slope at the coast due to the intensification of the eastward Guinea Current (Ingham 1979), or local cooling downstream of a cape (Marchal and Picaut 1977). Since local winds are not the driving force of this non-Ekman type upwelling, Cury and Roy (1987) used interannual anomalies of coastal sea surface temperature to estimate its intensity. The sign of anomalies was changed in their presentation so that a positive value was associated with a strong upwelling intensity.

The energy transferred through the water column by the wind creates turbulence in the surface layers. The rate at which turbulent kinetic energy of the wind is added to the surface layer is roughly proportional to the cube of the wind speed (Niiler and Kraus 1977; Elsbery and Garwood 1978). Therefore a wind mixing index that estimates turbulence in the upper layer is usually given by wind speed cubed (Bakun and Parrish 1980; Husby and Nelson 1982). Wind mixing indices, when available, were used (Peru, Morocco); otherwise wind speed (Senegal) or upwelling indices (proportional to wind speed squared) were used (California).

In Ekman-type upwelling, high wind speed enhances upward water movement and also generates turbulence in the surface layers. Therefore, off Peru, Morocco, and Senegal annual wind mixing index and upwelling intensity are positively correlated (Fig. 1). In non Ekman-type upwelling off Ivory Coast, Ghana where wind is not the driving force, annual wind mixing and upwelling intensity are independent variables (Fig. 2).

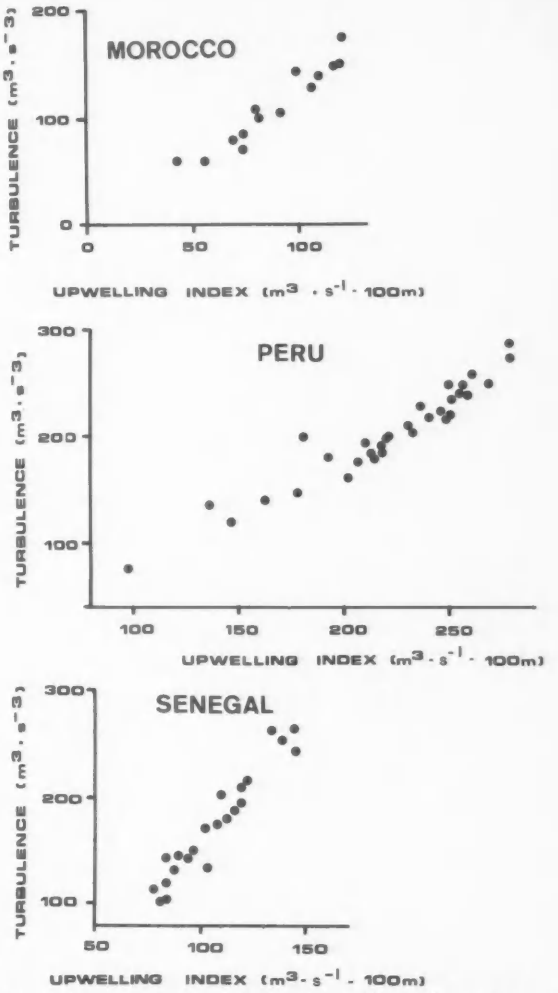

FIG. 1. Relationship between annual upwelling ($m^3 \cdot s^{-1} \cdot 100\ m^{-1}$ coastline) and turbulence ($m^3 \cdot s^{-3}$) indices for Ekman-type upwellings in Peru from 1953 to 1985 (Mendo et al. 1987), in Morocco from 1968 to 1981 (Belvèze 1984) and Senegal from 1964 to 1986 (C. Roy, unpubl. data).

Theoretical Approach

Acceptable food concentrations associated with stable ocean conditions must be present in the larvae's environment for survival (Lasker 1981a). Strong turbulence generated by high wind speed has a negative effect on larval survival by desegregating food and larvae patches (Saville 1965; Peterman and Bradford 1987) and on the recruitment (Lasker 1981a; Mais 1981). In an Ekman-type upwelling, vertical advection, new inputs of nutrients and turbulence (wind mixing) are linked with wind speed. Therefore in an Ekman-type upwelling, increasing upwelling intensity from weak to moderate should have a positive effect on recruitment since increased primary production would enhance food availability, wind mixing remaining low. Strong upwelling should have a negative effect on recruitment because wind mixing is high even if the primary production increases. This limitation should not exist in the case where the

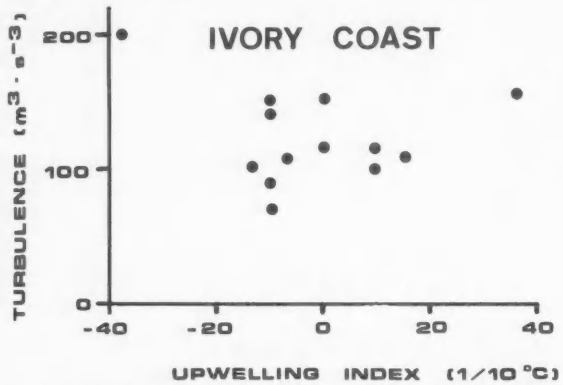

FIG. 2. Relationship between annual upwelling (1/10°C) and turbulence ($m^3 \cdot s^{-3}$) indices for a non Ekman-type upwelling in Ivory Coast, from 1966 to 1981 (1971 and 1972 are missing, Cury and Roy (1987) and ship of opportunity data).

strength of the upwelling is not correlated with wind intensity. We hypothesize that the relationships between recruitment variability and annual upwelling indices are dome shaped in Ekman-type upwellings (Fig. 3) and linear for non Ekman-type upwellings.

There are two limiting factors that explain the nonlinearity of the curve for Ekman-type upwelling. On the left side of the curve wind mixing is weak and the limiting factor is the production of food due to the low intensity of the upwelling; on the right side of the curve, the upwelling is strong and turbulence is then the limiting factor. There is therefore an "optimal environmental window" for moderate upwellings where the effects of the limiting factors are minimized (Fig. 3).

Statistical Method

In analyzing the relationship between recruitment and environmental factors most of the statistical methods are linear or an a priori transformation is used (essentially a logarithmic transformation) (Parrish and MacCall 1978; Anthony and Fogarty 1985; Stocker et al. 1985; Crecco et al. 1986). We applied a statistical technique developed by Breiman and Friedman (1985) that empirically estimates optimal transformations for multiple regressions. The response variable Y and the predictor variables $X_1,\ldots X_p$ are replaced by functions $T_1(Y)$ and $T_2(X_1),\ldots, T_{p+1}(X_p)$. A procedure estimates these functions T_i by minimizing

$$e^2 = \frac{E\{(T_1(Y) - \Sigma_{j=1}^{p} T_{j+1}(X_j))^2\}}{\text{Var}\,[T_1(Y)]}$$

An iterative algorithm (ACE: Alternating Conditional Expectation) permits the calculation of these transformation functions which do not belong to a particular parameterized family and which are even not monotone. It also differs from other empirical statistical methods usually used in that the transformations are unambiguously defined and estimated without use of ad hoc heuristics, restrictive distributional assumptions, or restriction of the transformation to a particular parametric family. If we fix the values of all but one variable and solve the problem of what new transformation will minimize the normalized residual sum of squares, then the solution is a conditional expectation that can be estimated empirically using a smoothing algorithm. The algorithm converges to an optimal solution and does not produce a given equation, but rather an empirical smoothed transformation of each of the data points for each of the variables. The transformation is not expressed in a particular unit (unless a functional transformation can be discerned from the plot) and its shape is found by plotting the transformed values of a variable versus the original values. This procedure, previously used in fishery studies by Mendelssohn and Cury (1987) and Mendelssohn and Mendo (1987) thus also provides a method for estimating maximum correlation, and gives new insights into the relationship between the response and predictor variables (i.e. it allows the identification of discontinuities in the relationship).

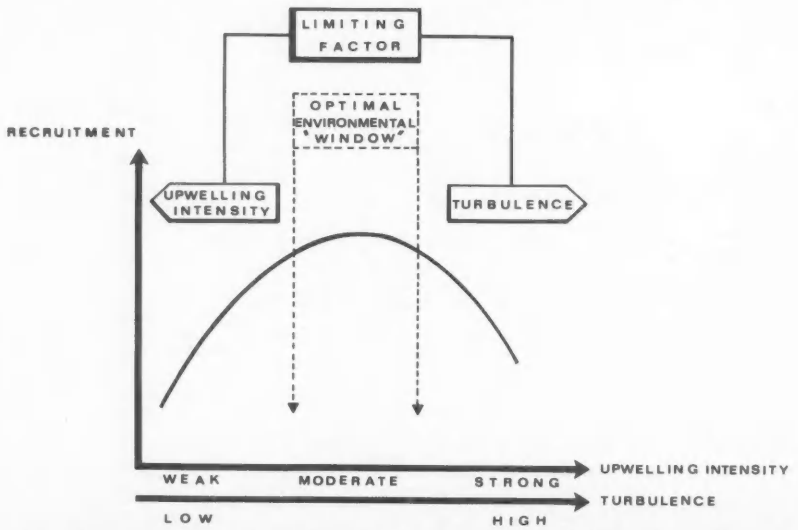

FIG. 3. Theoretical relationship between recruitment and environmental factors in upwelling areas.

TABLE 1. Recruitment (number of 3-mo-old fish) and mean annual parent stock (adult biomass of 3-mo or older fish) of the Peruvian anchoveta (Pauly et al. 1987). Annual turbulence and upwelling indices off Trujillo (Mendo et al. 1987).

Year	No. Recruits ($\times 10^9$)	Adult biomass (tons $\times 10^6$)	Turbulence index ($m^3 \cdot s^{-3}$)	Upwelling index ($m^3 \cdot s^{-1} \cdot 100\ m^{-1}$ coastline
1953	260	5.965	179	192
1954	252	9.378	229	236
1955	156	8.195	251	256
1956	106	5.017	259	261
1957	141	2.828	291	277
1985	172	3.661	221	239
1959	487	7.163	212	233
1960	573	11.618	199	220
1961	554	16.428	195	219
1962	394	14.688	188	217
1963	651	12.945	185	212
1964	364	14.183	185	217
1965	721	12.902	180	214
1966	635	15.175	221	250
1967	484	18.739	218	248
1968	352	12.859	273	278
1969	609	13.265	225	245
1970	568	14.428	250	268
1971	73	13.708	206	233
1972	105	3.106	239	254
1973	42	3.122	243	258
1974	22	3.446	148	177
1975	115	2.761	252	251
1976	90	4.420	238	250
1977	188	1.155	190	216
1978	209	3.878	163	202
1979	66	1.421	178	207
1980	392	2.504	201	181
1981	331	9.003	138	136

Review of some Pelagic Fish Stocks of Upwelling Areas

Peruvian Anchoveta

The idea that strong winds and turbulence in the upper layer can be detrimental to the survival of the Peruvian anchoveta (*Engraulis ringens*) was presented by Walsh et al. (1980). Using monthly anchoveta recruitment estimates, Mendelssohn and Mendo (1987) reinforced the idea of an effect of turbulence on short-term recruitment fluctuations. However, anchoveta recruitment also depends on the adult biomass level (Csirke 1980) and the dome shaped stock–recruitment relationship suggests a strong effect of parental cannibalism on anchoveta egg standing stocks (Santander 1987). The recruitment depends both on the parent stock and on environmental fluctuations.

We used the data updated in a recent synthesis on the Peruvian anchoveta stock (Pauly and Tsukayama 1987). These authors estimated a recruitment index (number of 3-mo-old fish) and adult biomass using virtual population analysis from 1953 to 1982 (Table 1). An annual turbulence index was calculated for one of the major anchoveta spawning areas located off Trujillo using monthly turbulence indices (wind speed cubed) of Mendo et al. (1987) (Table 1). Upwelling indices were not included in the calculation as they are strongly correlated with the turbulence indices (see Fig. 1) and do not improve fit.

Optimal empirical transformations (T1, T2, T3) for the multiple regression were calculated using the method previously described.

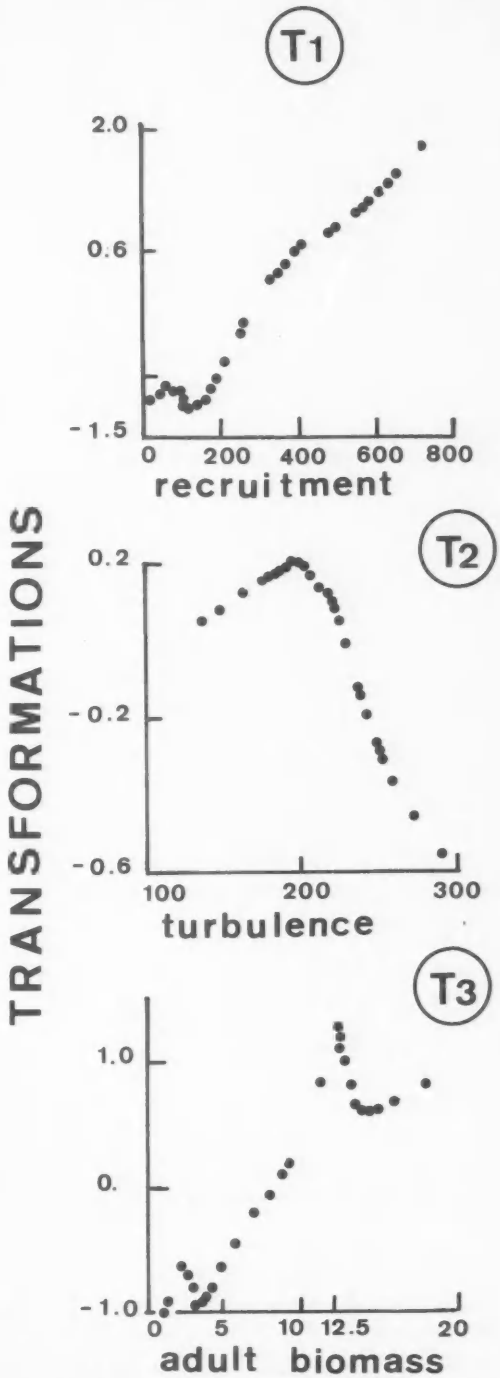

FIG. 4. Optimal empirical transformations for recruitment (No. of recruits $\times 10^9$) (T1), turbulence index ($m^3 \cdot s^{-3}$) (T2) and adult biomass ($t \times 10^6$) (T3) for the Peruvian anchoveta.

(1) T1 (Recruitment) = T2 (turbulence) + T3 (adult biomass).

TABLE 2. Recruitment (number of year class at age 2) and parent stock (adult biomass of 2-yr-old fish) of the Pacific sardine (MacCall 1979). Annual upwelling index off Monterey (Bakun 1973).

Year	No. Recruits ($\times 10^9$)	Adult biomass (tons·10^3)	Upwelling Index ($m^3 \cdot s^{-1} \cdot 100\ m^{-1}$) coastline
1946	1.625	566	92.8
1947	1.667	405	84.8
1948	3.875	740	78.1
1949	4.261	793	68.8
1950	3.690	780	70.1
1951	0.290	277	77.4
1952	0.397	136	68.7
1953	0.972	202	90.8
1954	1.197	239	81.3
1955	0.382	170	160.5
1956	0.264	108	139.8
1957	0.588	90	113.4
1958	1.586	177	97.1
1959	0.905	122	162.3
1960	0.288	88	91.6
1961	0.111	54	88.8
1962	0.074	27	94.8
1963	0.056	21	76.4
1964	0.011	11	152.8
1965		3	

The plot of the transformed values of the data against the original values are shown in Fig. 4. The estimated transformation of the recruitment is almost linear (Fig. 4, T1). Turbulence is transformed to a nearly dome shaped curve (Fig. 4, T2). It first increases to a value around 200 $m^3 \cdot s^{-3}$ (which corresponds to a wind speed between 5 and 6 $m \cdot s^{-1}$) and then decreases strongly. The transformation of parent stock is almost linear in shape with a small decrease for high values of adult biomass (higher than $12.5 \cdot 10^6$ t) (Fig. 4, T3). The resulting transformed model (1) explains 70% of the observed variance in the recruitment data. Recruitment is positively correlated with stock biomass; however, the relationship between recruitment and turbulence is non-linear. It suggests that the upwelling is beneficial for the recruitment until the wind speed reaches values of 5–6 $m \cdot s^{-1}$ and that for higher wind speed, turbulence has a negative effect on recruitment.

These transformations suggest that both high turbulence and low adult biomass may have played an important role in the collapse of the Peruvian anchoveta. In 1972 and 1973 the parent stock was low (Table 1) and produced few recruits which had difficulties surviving in an environment where turbulence was higher than 200 $m^3 \cdot s^{-3}$ (Table 1; Fig. 4, T2). Consequently, overfishing was apparently not the only factor preventing a recovery of the stock.

Pacific Sardine

The Pacific sardine (*Sardinops sagax caerulea*) fishery like the Peruvian anchoveta fishery is well documented. Analyses of the sardine stock–recruitment relationship (Clark and Marr 1955; Radovitch 1962; Murphy 1967) showed density dependence, often by assuming a Ricker functional relationship. Following Cushing (1971), who concluded that clupeoid stocks tend not to have strong density dependent regulatory mechanisms, MacCall (1979) showed that the stock–recruitment relationship presented no curvature (density-dependent regulation of the recruitment). We used new population esti-

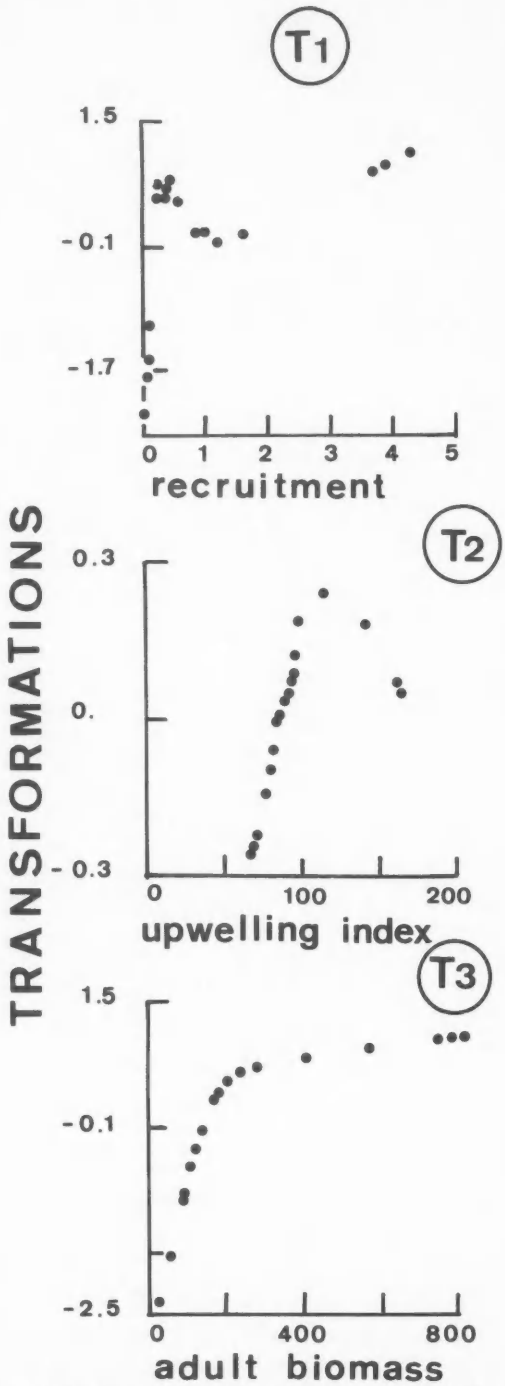

FIG. 5. Optimal empirical transformations for recruitment (No. of recruits $\times 10^9$) (T1), upwelling index ($m^3 \cdot s^{-1} \cdot 100\ m^{-1}$ coastline) (T2) and adult biomass ($t \times 10^3$) (T3) for the Pacific sardine.

TABLE 3. Recruitment (CPUE of age 0 group) of the Moroccan sardine (Belvèze 1984). Seasonal turbulence and upwelling indices off Tantan during the reproductive period (Belvèze 1984).

Year	CPUE (tons·d^{-1})	Upwelling index (m^3·s^{-1}·100 m^{-1}) coastline	Turbulence index (m^3·s^{-3})
1968	2.08	81.7	103.5
1969	2.15	42.1	61.0
1970	5.80	81.4	111.3
1971	1.38	56.1	60.2
1972	1.78	73.6	87.6
1973	0.89	73.6	71.1
1974	0.64	92.1	105.5
1975	0.96	120.3	155.8
1976	0.55	121.0	178.0
1977	0.46	116.6	152.9
1978	2.25	99.1	146.3
1979	0.63	69.1	79.1
1980	2.74	108.6	140.7
1981	0.78	105.6	128.7

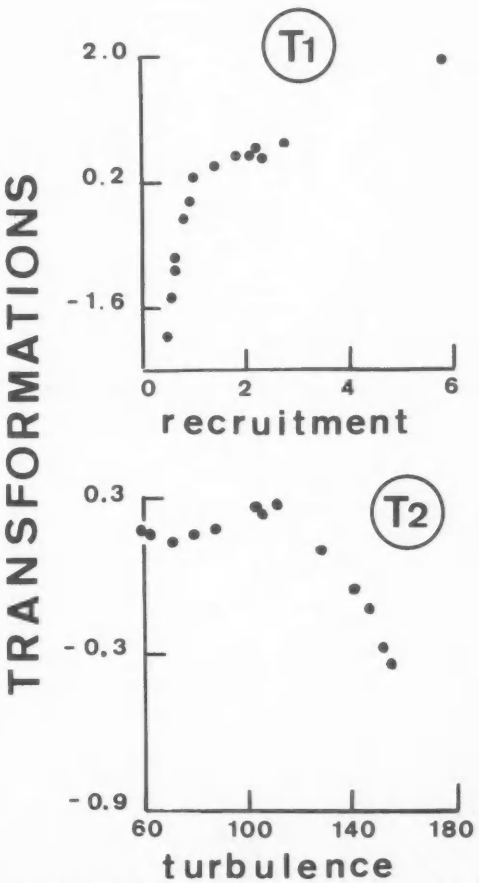

FIG. 6. Optimal empirical transformations for recruitment (t·d^{-1}) (T1) and turbulence index (m^3·s^{-3}) (T2) for the Moroccan sardine.

mates of the recruitments and Pacific sardine biomass calculated by MacCall (1979) (Table 2). The annual recruitment (year class at age 2) was estimated using a cohort analysis of aged landings data from 1945 to 1964. The adult biomass was calculated as all fish of age 2 or older. The only environmental data available were monthly upwelling indices off Monterey (36°N, 122°W) from Bakun (1973) that were averaged over the whole year (Table 2).

Optimal transformations (T1, T2, T3) for the multiple regression were calculated using the current year upwelling index and adult biomass, and year class at age 2 for recruitment 2 yr later. For example recruitment index in 1948 is associated with annual upwelling index and adult biomass calculated in 1946

(2) T1 (recruitment) = T2 (upwelling index) + T3 (adult biomass).

The transformation for the recruitment index presents a sharp increase for low values (under $0.5 \cdot 10^9$ fish), it decreases for values between 0.5 and $1.0 \cdot 10^9$ and increases slowly for higher values (Fig. 5, T1). The upwelling index transformation is dome shaped with a breaking point around a value of 100–120 m^3·s^{-1} per 100 m of coastline (this value corresponds roughly to an alongshore wind speed of 5 m·s^{-1}) (Fig. 5, T2). The transformation of adult biomass is typically a Beverton and Holt stock–recruitment relationship (Fig. 5, T3); it shows a curvature for sardine biomass of $200 \cdot 10^3$ metric tons. Model (2) explains 87% of the recruitment variance.

These relationships provide some complementary information on the waning years of the Pacific sardine fishery. After 1954, the adult biomass was under $200 \cdot 10^3$ metric tons (Table 2) and the recruitment–adult biomass relationship was on a slope where a minor stock produced a minor recruitment. After 1954, the upwelling intensity was higher than in the past (Table 2), and may have had a negative effect on recruitment. MacCall (1983) suggested that the rate of decline was sustained because the fishery consistently exceeded sustainable yields. The transformations of the Ekman index and the adult biomass suggest that this was not the only factor producing the collapse. It may have been due to a conjunction of several depressive factors on recruitment; excessive upwelling, or too depressed biomass associated with a high exploitation rate.

West African Sardines and Sardinellas

Morocco

For Morocco, a recruitment index for sardine (*Sardina pilchardus*) may be obtained by using CPUE (Catch Per Unit of Effort) of age 0 and age 1 of the following year (Belvèze and Erzini 1983; Belvèze 1984) (Table 3). Monthly turbulence indices at 28°N, 13°W from October to April (Belvèze 1984) were used to calculate an annual wind mixing index during the reproductive and larval growth periods.

Optimal transformations (T1, T2) are estimated for the simple regression between recruitment and turbulence.

(3) T1 (recruitment) = T2 (turbulence).

The model explains only 21% of the observed variance in recruitment. An estimation of stock size is not available and it would certainly contribute to an explanation of a much greater part of the variance if included in the model. However, the transformation of recruitment (Fig. 6, T1) is very close to a log transformation. The transformation of the turbulence appears to increase very slowly to a value of 120 m^3·s^{-3} (which corresponds to a wind speed close to 5 m·s^{-1}); for higher values of wind speed it decreases strongly (Fig. 6, T2).

TABLE 4. CPUE, fishing effort for the Senegalese round sardinella fishery (Fréon, 1983). Seasonal wind speed, turbulence, and upwelling indices off Yoff (Fréon 1983; C Roy, unpubl. data).

Year	CPUE (tons·10 h^{-1})	Effort 10 h·10^3	Wind speed ($m \cdot s^{-1}$)	Turbulence index ($m^3 \cdot s^{-3}$)	Upwelling index ($m^3 \cdot s^{-1} \cdot 100\ m^{-1}$)
1964				152	97
1965				178	113
1966	13.54	0.607	4.90	145	90
1967	11.62	0.673	4.66	144	84
1968	12.70	0.880	4.46	105	85
1969	9.86	1.325	4.37	120	83
1970	7.56	1.469	4.29	133	87
1971	10.68	1.262	5.01	176	109
1972	16.32	1.455	6.00	255	137
1973	11.38	2.590	5.30	211	117
1974	9.78	3.509	5.99	241	144
1975	7.22	4.062	5.50	218	122
1976	8.06	4.820	5.93	261	134
1977	8.61	5.157	5.61	202	111
1978	9.15	4.913	5.01	172	103
1979	6.68	5.996	4.53	115	78
1980	7.01	6.203	5.21	186	115
1981	6.09	7.773	5.03	135	103
1982	2.30	10.206	4.77	142	93
1983	2.00	10.841	4.51	106	82
1984				135	104
1985				265	144
1986				194	119

TABLE 5. CPUE, fishing effort for the Ivoiro-ghanaian sardinellas fishery (Cury and Roy 1987, unpubl. data). Annual turbulence (C. Roy, unpubl. data) and upwelling index off Abidjan (Cury and Roy 1987).

Year	CPUE (tons·d^{-1})	Effort (d·10^3)	Turbulence index ($m^3 \cdot s^{-3}$)	Upwelling index (1/10°C)
1965				29.7
1966	7.33	3.420	91	−9.3
1967	8.51	3.746	111	15.8
1968	7.35	4.073	70	−10.6
1969	5.30	3.616		−18.3
1970	3.81	5.716	117	7.5
1971	4.64	5.484		7.8
1972	6.47	3.930		4.5
1973	3.29	2.483	200	−37.8
1974	4.87	2.024	113	−6.8
1975	7.96	1.768	155	0.8
1976	10.64	1.824	158	36.1
1977	12.23	2.003	120	1.2
1978	9.26	2.200	103	9.4
1979	6.53	2.681	105	−13.2
1980	5.75	2.409	142	−10.7
1981	9.52	2.207	151	−9.9

Senegal and Ivory Coast-Ghana

In Senegal and Ivory Coast-Ghana, recruitment indices are not available for Sardinellas (*Sardinella aurita* and *Sardinella maderensis*). Fréon (1983) and Cury and Roy (1987) studied pelagic fish stocks in these upwelling areas and showed that annual CPUE is a function of fishing effort and of the upwelling intensity during the fishing year and 1 yr before. The upwelling intensity 1 yr before the fishing year appears to have an important effect on recruitment (sardinellas are recruited to the fishery after 1 yr). In Senegal, the upwelling is an Ekman-type upwelling and wind speed is used as an upwelling index (Fréon 1983). The monthly averages of the wind speed over the upwelling season (November to May) were used to estimate interannual upwelling intensity and wind mixing. In Ivory Coast-Ghana, the upwelling is not caused by the local wind and sea surface temperature anomalies (deviation from a mean cycle during the upwelling seasons) were used as an upwelling index (Cury and Roy 1987). CPUE, fishing effort, upwelling or turbulence indices are presented in Table 4 for Senegal and Table 5 for Ivory Coast-Ghana.

Optimal transformations (T1, T2, T3, T4) for the multiple regression between CPUE and fishing effort, environmental indices during the fishing year and 1 yr before are calculated

$$(4)\quad \mathrm{T1}(\mathrm{CPUE}_i) = \mathrm{T2}(\text{fishing effort}_i) + \mathrm{T3}(\mathrm{ind.}_i) + \mathrm{T4}(\mathrm{ind.}_{i-1})$$

where i = year index, ind. = upwelling index (Ivory Coast-Ghana) or wind speed (Senegal).

For Senegal and Ivory Coast-Ghana the models explain respectively 97 and 94% of the observed variance in CPUE. Empirical transformations of CPUE for Senegal and Ivory Coast-Ghana are curved and suggest that a log transformation is suitable (Fig. 7, T1 and Fig. 8, T1). The transformations of effort are nearly linear and have a negative slope. The relationship between CPUE and effort is negative and can be approximated with a linear model (Fig. 7, T2 and Fig. 8, T2). The transformation of upwelling index or wind speed during the fishing year increases for Ivory Coast and Senegal and shows a platform for Senegal (Fig. 7, T3 and Fig. 8, T3). The contribution of this index to the explication of the CPUE variance was interpreted as the effect of availability of the fish; fish seem less available during strong upwelling. The models used by Fréon (1983) and by Cury and Roy (1987) to analyze CPUE in Senegal and in Ivory Coast empirically integrate the upwelling index 1 yr before fishing to evaluate recruitment. Therefore analyzing the form of the transformation of this parameter that maximizes the correlation in the model allows us to identify

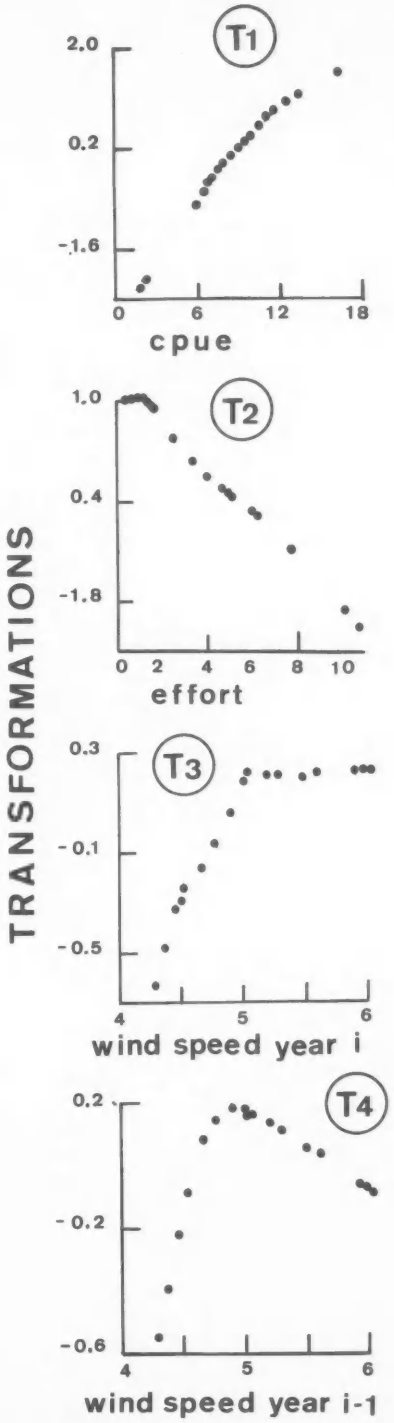

FIG. 7. Optimal empirical transformations for CPUE ($t \cdot d^{-1}$) (T1), fishing effort ($10\ h \times 10^3$) (T2), wind speed ($m \cdot s^{-1}$) during the fishing year (T3) and wind speed during the previous year (T4) for the Senegalese round sardinella.

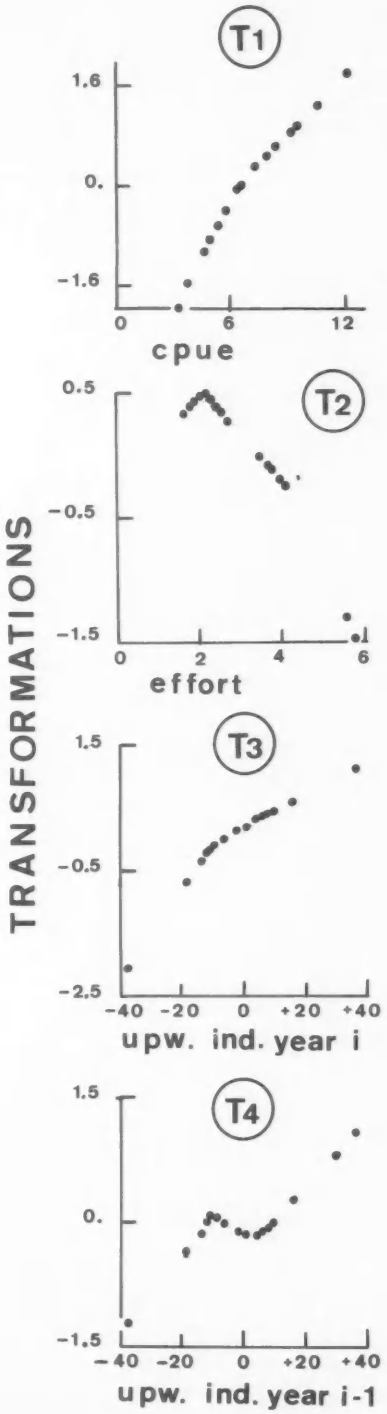

FIG. 8. Optimal empirical transformations for CPUE ($t \cdot d^{-1}$) (T1), fishing effort ($d \cdot 10^3$) (T2), upwelling index (1/10°C) during the fishing year (T3) and upwelling index during the previous year (T4) for the Ivoirian sardinellas.

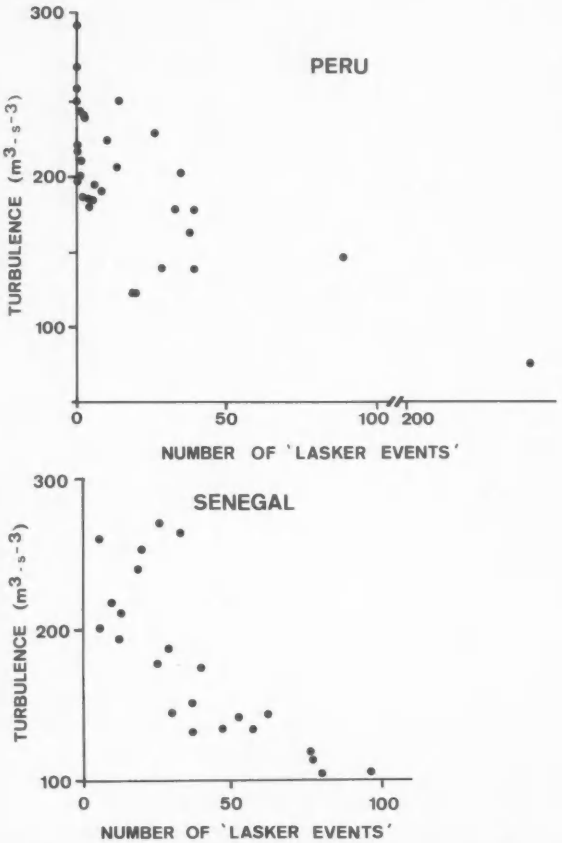

FIG. 9. Relationship between annual turbulence indices ($m^3 \cdot s^{-3}$) and occurrence of "Lasker events" in Peru and Senegal (from Mendelssohn and Mendo (1987) and C. Roy, unpubl. data). The number of "Lasker events" measures the number of 4-d periods during which the wind speed did not exceed 5 $m \cdot s^{-1}$ (see Peterman and Bradford (1987) for details about the calculation).

the relationship between the environmental parameter and recruitment. For Senegal, the transformation of wind speed 1 yr before the fishing year is dome shaped with a breaking point centered at 5 $m \cdot s^{-1}$ (Fig. 7, T4). For the Ivory Coast-Ghana the transformaton of the upwelling index is nearly linear with just a platform for values around zero (Fig. 8, Table 4). This suggests that recruitment and upwelling are positively correlated in Ivory Coast-Ghana.

The transformations of the indices that evaluate upwelling intensity in Senegal and in Ivory Coast-Ghana are consistent with our hypothesis that a linear relationship exists between recruitment and upwelling in a non Ekman-type upwelling and that a dome shaped relationship exists in an Ekman-type upwelling.

Discussion: "5–6 $m \cdot s^{-1}$ Wind Speed" as an "Optimal Environmental Window"

"Lasker Events" and Average Seasonal Wind Speeds

Peterman and Bradford (1987) and Mendelssohn and Mendo (1987) used an index reflecting Lasker's hypothesis (1978), called the "Lasker event". It measured the number of 4-d periods during which the wind speed did not exceed 5 $m \cdot s^{-1}$. While arrived at from different time scale studies, our results are also consistent with these previous studies which present evidence of the importance of this criterion and its impact on larvae survival.

Husby and Nelson (1982) noted that ..."the average intensity of turbulent wind mixing over a spawning season is not likely to be well correlated with interannual variability in recruitment. Rather, the existence of sufficient time–space windows within which turbulence does not exceed critical values may be the relevant factors." The validity of this assumption based on Lasker's (1978) hypothesis is confirmed by the result of Peterman and Bradford (1987); these authors show that it is the succession of calm periods more than the mean wind speed that is correlated with daily larval mortality rates. Our results are in agreement with these observations; Fig. 9 shows that the number of Lasker events during an upwelling season is negatively correlated with the average wind speed cubed for Peru and Senegal (data not available for the other areas). Therefore, wind speed on average over a spawning season could be used as a rough index of the number of low turbulence events during the spawning season.

Physical and Biological Significance of 5–6 $m \cdot s^{-1}$

What is the significance of the 5–6 $m \cdot s^{-1}$ value considering oceanographic features and enrichment processes? From a physical point of view, the threshold wind speed of 5 $m \cdot s^{-1}$ is a value at which wind stress begins to exert a measurable mixing effect on the surface layer in near-shore waters (Kullenberg 1971, 1972, 1974, 1976, and 1978). Also, when the wind speed is greater than about 7 $m \cdot s^{-1}$, wave breaking becomes obvious (Pond and Pickard 1978) and generates strong turbulence. From a biological point of view, wind speed of approximately 5 $m \cdot s^{-1}$ has been found to be a "threshold" value above which wind mixing tends to desegregate phytoplankton patchiness (Therriault and Platt 1981; Demers et al. 1987). These authors demonstrate that if the winds are strong enough to surpass this threshold for surface layer mixing, wind mixing dominates all other potential sources of variance of the phytoplankton patchiness; below this threshold the phytoplankton patchiness can be ascribed to biological causes. The threshold effect on recruitment success is consistent with this observed dynamic of phytoplankton.

Dispersion might not be the only factor affected by strong wind mixing. Huntsman and Barber (1977) showed that primary production and zooplankton biomass in the Northwest African upwelling is also affected by strong wind mixing. They show that strong winds produce a strong mixed layer and a light limited phytoplankton population. Therefore larval survival in the case of strong wind mixing could also be affected by the reduction of primary production.

Increased offshore transport of eggs and larvae with increased upwelling intensity is often cited as a cause of larval mortality (Bakun and Parrish 1980; Parrish et al. 1983). At this stage of this analysis it is impossible to know the relative importance of this detrimental factor. Since reproductively active fish avoid areas with strong offshore Ekman transport (Parrish et al. 1983; Husby and Nelson 1982; Roy et al. 1989), we think that turbulence in a reproductive area is perhaps a dominant factor.

Validity of the Theory

Review of information on some of the most important and well studied pelagic fish stocks of upwelling areas indicates that

the facts are consistent with the theory. When calculating the transformations of the different variables, taken one by one, like recruitment with parent stock or recruitment with upwelling (plots not presented here), it appears that each variable explains a significant percentage of recruitment variance and also that the transformations are similar to those obtained when simultaneously analysing recruitment, parent stock, and upwelling. Stock–recruitment and recruitment–upwelling relationships are both important for recruitment success. For an Ekman-type upwelling, the optimal transformations of turbulence (or upwelling index) in the Peruvian, Californian, Moroccan, and Senegalese ecosystems are very close to those predicted by theory. A dome shaped relationship exists between recruitment and upwelling intensity estimated from wind data. The non-linearity always appears for values of wind speed around 5–6 $m \cdot s^{-1}$. This value is common for all the transformations and suggests that for different Ekman-type upwelling ecosystems there is a common and optimum wind mixing level in the stable layers of the upper ocean.

The validity of the theory is reinforced by the results obtained in Ivory Coast-Ghana. In this ecosystem local trade winds are weak and not correlated with upwelling intensity. Our theory suggests that strong wind mixing becomes a limiting factor even if upwelling intensity enhances primary production, but that if this limiting factor is not present, primary production and availability of food is the only limiting factor and recruitment should increase with upwelling intensity. The transformations, obtained with Ivory Coast-Ghana data, clearly illustrate that recruitment and upwelling intensity are almost linear and positively correlated.

Conclusion

Upwelling intensity differs from one area to another. In a given upwelling area, pelagic fish reproductive strategy tends to reach the optimal environmental window (as defined by our theory) by locally optimizing physical constraints. For example, in a weak upwelling area fish tend to reproduce in the most productive time–space areas. In the case of a moderate upwelling, fish reproductive strategies have to compromise between high productivity and strong turbulence. In the case of a strong upwelling, the turbulence is the only limiting factor for recruitment. Thus, local optimal environmental parameters may differ from one area to another and recruitment can be sometimes positively or sometimes negatively correlated with upwelling intensity. In upwelling areas the "match-mismatch" or "stability hypothesis" theories should both be valid considering our general relationship between recruitment success and environmental limiting factors.

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Effects of Forest Harvesting on Spawning Gravel and Incubation Survival of Chum (*Oncorhynchus keta*) and Coho Salmon (*O. kisutch*) in Carnation Creek, British Columbia

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Scrivener, J. C. and M. J. Brownlee. 1989. Effects of forest harvesting on spawning gravel and incubation survival of chum (*Oncorhynchus keta*) and coho salmon (*O. kisutch*) in Carnation Creek, British Columbia. Can. J. Fish. Aquat. Sci. 46: 681–696.

Following logging, pea gravel and sand (i.e. fines) in the stream bed of Carnation Creek, British Columbia increased 4.6 and 5.7%, respectively. The quantity of fines was greater in the bottom layer, while the frequency and magnitude of changes in composition were greater in the top layer of streambed cores. Changes in streambed fines depended on the timing and type of streamside logging and on the timing of large freshets. Accumulating fines appeared to originate from erosion of streambanks or from upstream storage areas and they were transported as bedload. Suspended sediment (11.4–44.5 $t \cdot km^{-2} \cdot yr^{-1}$) did not increase after road construction or logging. Deposition and scour rates of pea gravel and sand in the streambed were inversely related to particle size, and to their depth in the bed. Following logging, survival to emergence declined from 29.1 to 16.4% for coho salmon (*Oncorhynchus kisutch*) and from 22.2 to 11.5% for chum salmon (*O. keta*). Annual mean survival to emergence and size of fry of both species were positively related to two indices of substrate composition. Annual changes in substrate composition and peak flows explained 60 and 73% of the variability in survival to emergence for chum and coho salmon, respectively.

Après l'exploitation forestière, la quantité de gravier fin et de sable (c'est-à-dire de particules fines) sur le lit du ruisseau Coronation, Colombie britannique a augmenté respectivement de 4,6 et de 5,7 %. La quantité de particules fines était supérieure dans la couche du fond, tandis que la fréquence et l'amplitude des variations de composition étaient supérieures dans la couche du haut des carottes prélevées dans le lit. Les variations dans la nature des particules fines du lit dépendaient du moment de l'exploitation forestière le long du cours d'eau et du type, et non pas du moment où s'étaient produites d'importantes availaisons. Les particules fines semblaient provenir de l'érosion des rives ou de lieux d'accumulation en amont et ont été transportées sous forme de charge de fond. Les sédiments en suspension (11,4 à 44,5 $t \cdot km^{-2} \cdot an^{-1}$) n'ont pas augmenté après la construction des routes ou l'exploitation forestière. Les taux d'accumulation et d'érosion des graviers fins et des sables dans le lit du cours d'eau étaient inversement proportionnels à la taille des particules et à leur profondeur dans le lit. À la suite de l'exploitation forestière, la survie jusqu'au moment de l'émergence a diminué de 29,1 à 16,4 % pour le saumon coho (*Oncorhynchus kisutch*) et de 22,2 à 11,5 % pour le saumon keta (*O. keta*). La survie moyenne annuelle jusqu'à l'émergence et la taille des alevins étaient liées de façon positive à deux indices de la composition des matériaux du fond. Des variations annuelles de la composition des matériaux du fond et des débits de pointe ont expliqué, respectivement, 60 et 73 % de la variation de la survie jusqu'à l'émergence des saumons keta et coho.

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Much has been written about changes in fluvial processes and sediment production associated with timber harvesting (Anderson 1971; Gibbons and Salo 1973; Iwamoto et al. 1978). Some influences of fine particles on survival, emergence, and fitness of salmonid embryos and emerging fry are also known (Koski 1966, 1975; Hall and Lantz 1969; Phillips 1971). More recently the sources of fines, sedimentation processes, and the influence of sediment on fish production have been investigated (Beschta and Jackson 1979; Cederholm et al. 1981; Meehan and Swanston 1977). By understanding these fluvial processes and their influence on fish production, better forest management plans can be developed that protect aquatic habitat.

Sediment composition affects two critical properties of spawning gravel: permeability and porosity. Permeability affects delivery and removal rates of oxygen, carbon-dioxide, and other metabolites (Wickett 1958; McNeil and Ahnell 1964), which influence survival (Alderdice et al. 1958; Reiser and Bjornn 1979; Rombough 1983). Small pore size can restrict intergravel movement of alevins and create a barrier to emergence (Dill and Northcote 1970; Phillips 1971; Phillips et al. 1975).

The objectives of the Carnation Creek studies of spawning gravel are to assess the effects of current forest harvesting prac-

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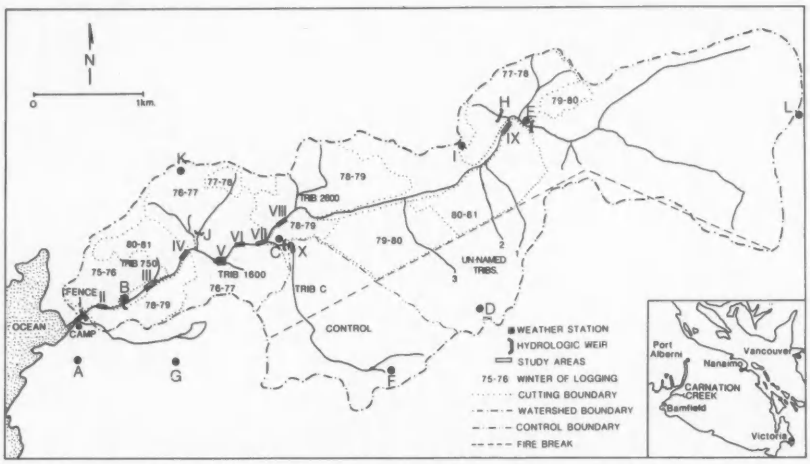

FIG. 1. Location of Carnation Creek (inset) and a detailed map of the watershed showing locations of stream study sections, fish counting fence, and boundaries of logging cutblocks.

tices on spawning gravel composition, intergravel dissolved oxygen levels, and permeability (Scrivener and Brownlee 1982), and the influence of these features on the survival and size of emerging fry. Long-term objectives are to understand influences on the abundance and production of these natural stocks of coho (*Oncorhynchus kisutch*) and chum salmon (*O. keta*). Variations in sediment yield, sources of sediments, and other fluvial processes were also investigated during a 14-yr study series (1973–86) and they provide some insight about the accumulation and scour rates of different particle sizes in a natural streambed. A more detailed study of the intertidal area of Carnation Creek where chum salmon spawn at higher densities has been reported elsewhere (Scrivener and Brownlee 1982; Scrivener 1988a).

Watershed and Study Description

Carnation Creek is a small stream that enters Barkley Sound on the west coast of Vancouver Island (Fig. 1). The stream drains an area of ~10 km^2 in the Coastal Hemlock Zone of British Columbia (Hartman et al. 1987). Annual precipitation is 250–480 cm. Stream flows are highly variable seasonally, ranging from 0.025 $m^3 \cdot s^{-1}$ in summer to 33 $m^3 \cdot s^{-1}$ in winter during most years. Peak flows of 37, 44, and 64 $m^3 \cdot s^{-1}$ with return periods of 5, 12, and 30 yr, respectively have been observed during the study (Hetherington 1982, 1988). Air temperatures below 0°C were recorded for only a few $d \cdot yr^{-1}$ so freezing of incubating salmon eggs was of little concern.

Topographically the basin features rugged terrain of steep slopes to 700 m elevation and a narrow valley bottom through which the stream meanders. Slope soils are shallow, coarse textured, and highly organic (Oswald 1973). Bedrock is of volcanic origin, and the region was glaciated during the Pleistoscene. Soils in the valley bottom are derived from recent alluvium and they are underlain by gravel deposits (as deep as 4 m), bedrock, and some sandy clay deposits.

Anadromous fish utilize the lower 3.2 km of the stream, encompassed by study sections I and VIII (Fig. 1). Most chum salmon spawn intertidally (section I), while a few chum salmon (3–30% of the total run), all coho salmon and all steelhead trout (*Salmo gairdneri*) passed through the counting fence (Fig. 1) to spawn (sections II to VIII). Mean gradient is 0.9% in the lower 3.2 km of stream and the bed consists of gravel with very few cobbles (>100 mm diameter; Scrivener 1975). Numerous fallen trees and buried logs occur in the channel both singly and in clusters providing fish habitat (i.e. LOD). Extensive gravel bars indicate considerable gravel movement. From 3.2 to 4.1 km, the stream is confined to a narrow bedrock canyon with an average gradient of 8.4%. The channel contains numerous logjams with gravel accumulations behind them. The next segment of stream, 4.1 km to E-weir (study section IX, Fig. 1) contains resident cutthroat trout (*S. clarki clarki*), and flows over a gravel substrate with some cobbles (100–200 mm).

The Carnation Creek Watershed project was initiated in 1971 as a 16-yr study. It consisted of prelogging (1971–75), logging (1976–spring 1981), and postlogging (1982–86) periods. It has now been extended until 1991. The logging plan contained three basic treatments.

(1) Leave-strip treatment — Area 1 (sections II–IV) was logged as three openings during 1976 (23 ha), 1978–79 (19.4 ha), and 1980–81 (16 ha). This left the lower 1300 m of Carnation Creek with a narrow strip of deciduous vegetation and ~200 merchantable trees along its banks. (Fig. 1).

(2) Intense streamside treatment — Area 2 included the next 900 m of stream (sections V and VI). It was logged in 1976–77 as two clearcuts (61, 34.4 ha). Streamside alders were girdled and injected with Tordon 22K herbicide. All merchantable trees were felled away from the channel, or if leaning over it, they were felled across and then yarded away from the stream to roadside landings. Streambanks and large debris in the channel were broken, scared and destabilized (Toews and Moore 1982).

(3) Careful streamside treatment — Area 3 (section VIII) was logged as two clearcuts (63, 13 ha) during 1978–79. Minor vegetation such as salmonberry was left; only six merchantable trees that could not be jacked or cabled were felled across the channel and removed. Streamside alder was felled and during scarification the logging debris was piled for burning. Gravel samples from this treatment area included cores from study section VII, because it was on the border of areas 2 and 3 (Fig. 1).

Study section IX was included as a fourth area, because the streambed contained coarser material and the timing of treat-

ments was different than among the sections used by anadromous fish. The area adjacent to section IX was not logged until 1980–81 (Fig. 1). Clearcuts were completed on small tributaries upstream of section IX in 1977–78, but little change in the main stream was apparent.

About 41% of the watershed had been logged upon completion of the last clearcut in April 1981. Here, high-lead systems such as steel spars and grapple yarders were used to log between November and April. A more detailed description of the logging plans and study sections is available elsewhere (Dryburgh 1982; Scrivener and Brownlee 1982; Toews and Moore 1982).

Materials and Methods

Collection and Processing of Physical Data

Since 1973, samples of the streambed have been obtained from study sections II to IX during low flows of summer as part of an annual physical survey. During 1971, permanent survey hubs were established at 3-m intervals in each study section (Toews and Moore 1982). Forty-five hubs that were located at potential spawning sites were chosen for sampling (4–10·section^{-1}). Another 25 sites (hubs) were chosen for sampling during 1976 when access became easier ($\geq$8·section^{-1}). Gravel samples were obtained from the cross sections of these hubs each year.

A modification of Ryan's (1970) freeze-core technique was used to sample the streambed. A 5-cm diameter steel probe attached to a sampling "pot" was driven 30 cm into the bed. Acetone and dry ice were added to the pot and the super-cooled acetone froze a gravel core 20–30 cm in diameter around the probe in ~25 min. The frozen cores, weighing 8–22 kg, were split into top (1–15 cm) and bottom (15–30 cm) layers, and bagged separately for particle size analysis. The diameter of the cores was larger than the largest rocks thereby reducing the bias of the weight of these rocks in the samples (Shirazi et al. 1981).

Each layer was oven dried at 105°C, and the largest and smallest diameter of the largest rock measured. The sample was then split one to four times depending upon its weight, and particles too large to pass through the sample splitter (25 mm) weighed. Split samples were weighed and one of them was passed through five nested sieves (9.55, 2.38, 1.19, 0.297, and 0.074 mm). The separated portions were weighed and the data stored in computer files. An indicator of the largest rock size in each layer (<150, <100, or <50 mm) was also stored in the files. During a few early years, weights retained by the sample splitter were not recorded separately. This analysis separated the sample into gravel; pea gravel; coarse, medium, and fine sand; and silt-clay components as classified by the U.S. Department of Agriculture (Scrivener and Brownlee 1982).

During 1982, dissolved oxygen (DO) was measured in the summer prior to gravel sampling at the original 45 sites sampled that year. A stainless steel syringe was used to slowly extract 700 mL of inter-gravel water from a depth of 20 cm. Surface stream water was also sampled at a number of locations in each study section. A Hach Kit was used to measure DO of the sample to the nearest 0.1 mg·L^{-1}. In order to reduce variability among DO concentrations that was caused by diel fluctuations of water temperature or of stream flow during the 4-d sampling period, concentrations were expressed as a percentage of mean surface DO.

Five measures of peak flow representing different periods of egg incubation were used as indicators of annual variation of potential streambed scour. They were obtained from the hydrological weir at station B where water levels have been recorded continuously since April 13, 1971 (Fig. 1). Water Survey of Canada methods and software were used to digitize the charts and to compute flows (Ozga 1974). Stage–discharge curves were checked and updated at least five times each year with measurements from a control cross section near the weir. These measures of peak flow were: (1) October 20 to January 15, and (2) October 20 to January 31, because adult chum salmon entered Carnation Creek and spawned between October 20 and November 5 (Andersen 1983, 1984, 1985), (3) November 16 to January 15, and (4) November 16 to February 15, because adult coho entered the stream in November, at an unripened stage and began spawning about 2-wk later (Holtby et al. 1984), and (5) annual peak flow (October–March) as an indicator of annual variation in scour potential. Flows from February to the time of fry emergence (April) were excluded from most of the measures of peak flow because other studies have indicated that the behaviour of salmon larvae at this time might make them less susceptible to scour (Bams 1969; Dill 1969).

Measurements of suspended sediment transport were also obtained at B-weir with a battery powered pumping sampler. Samples were pumped from a fixed point ~10 cm above the bed at intervals that were regulated by stream flow. During a number of freshets each year, these point samples were related to total stream transport by a series of depth integrated samples from various distances across the width of the channel. Size analyses of suspended particles were obtained for samples from some of these storms. Sediment hydrographs were obtained in this manner from 1973 to 1986 (ANON, 1973–85). Total suspended sediment that was transported and total volume of stream flow were then calculated for each water-year (October 1–September 30).

Collection and Processing of Biological Data

Annual egg-to-fry survival was estimated from calculated egg deposition and enumeration of emergent fry. Potential egg deposition was calculated from the number and fork length (FL) of all adult females at the counting fence, and fecundity relationships for chum (Egg No. = 69.6·(FL in cm) − 2361.1, n = 32, r = 0.73, $p<0.001$; Hartman 1981) and coho salmon ($\log_{10}$Egg No. = 2.786·$\log_{10}$(FL) − 1.730, r = 0.82, n = 45, $p<0.001$). The numbers of emerging chum salmon fry were obtained from counts at the downstream migrant traps of the fence (Fig. 1). Coho fry enumeration was based on a May population estimate in the stream after emergence and fence counts prior to the May census (Scrivener and Andersen 1984). All migrant fry were counted at the fence except during freshets when only a portion of the flow could be sampled. Egg-to-fry survival of chum salmon was not obtained for 1983–1984, because no unspawned females passed through the fence that year.

Mean FL of emerging coho and chum salmon were assumed to be the same as fry emigrating through the counting fence. During prelogging years (1973–76), fry first appeared at the fence in April, but they began appearing in March after 1976 (Scrivener and Andersen 1984). Measurements were obtained every 7–10 d thereafter from at least 50 fry of each species. Mean FL and fry counts of each sampling date were used to calculate a weighted annual mean during the first 50 or 60 d of movement. Chum fry emigration usually ended in ~50 d, and

fry sizes were similar to those caught in intertidal emergence traps (Scrivener 1988a). The size of coho fry at the fence did not increase until after the first 60 d of movement (Andersen 1983, 1984, 1985, 1987), so growth had not affected the lengths significantly. A sampling period of 60 d was also judged representative, because coho salmon spawned over a long period (20–60 d; Holtby et al. 1984), and because coho fry have been shown to emerge from most individual redds during an extensive period (48–60 d; Tagart 1984).

The size of emerging fry is influenced by the egg size for both coho (Beacham et al. 1985) and chum salmon (Koski 1975; Beacham and Murray 1985). If environmental impacts on fry size are being studied, egg size should be kept constant or corrections for its variability should be made (Koski 1975). Egg size and fecundity are both functions of adult female length (Allen 1958; Koski 1975), so mean egg size each year could be predicted from mean length of spawning females. Mean size of chum salmon eggs was calculated for those fish that went through the counting fence each year by using the fecundity relationship mentioned earlier and the relationship between female length and egg weight (Egg weight in mg = 5.587 · (FL in cm) − 52.31, $r = 0.65$, $n = 31$, $p<0.001$). Predicted mean size of fry was then calculated for each year (Fry FL = 18.30 + 0.0633 · Egg weight, $r = 0.63$, $n = 99$, $p<0.001$; data from Beacham et al. 1985). Annual variability in fry size that was attributable to annual variability in egg size was obtained by subtracting fry length predicted from egg size each year from fry length predicted for 1973 (year of median female size). These values (−0.8 to +1.1 mm) were added to the mean size of fry of their year. Carnation Creek coho salmon that were obtained for fecundity estimates were not mature enough for estimating egg weights, so data from the literature and the fecundity relationship were used to predict annual mean diameter of coho eggs (Egg diameter in mm = 5.423 + 0.0294 · (FL in cm), $r = 0.63$, $n = 61$, $p<0.001$; data from Allen 1958). Volume was calculated as a prolate spheroid (Groot and Alderdice 1985) by

$$\text{mL} = 4/3\ \pi\cdot(\text{diameter}/2.0)^2\cdot(\text{diameter}_2/2.0),$$

and weight was calculated by

$$\text{mg} = \text{mL}\cdot 1.062,$$

(D. Alderdice, Pacific Biological Station, Nanaimo, B.C., pers. comm.). Predicted size of fry was then calculated for each year (Mean FL = 26.83 + 0.0338·Egg weight, $r = 0.72$, $n = 107$, $p<0.001$; data from Beacham et al. 1985), and differences in size of coho salmon fry due to annual variability in egg size (−0.4 to 0.4 mm) was used to correct mean size of fry as done with chum salmon.

Data Analysis

Initial analysis was suited to a three-way ANOVA, because the gravel sampling program was designed to compare: (1) layers within the cores (top and bottom), (2) different streamside treatments (areas 1 to 4), and (3) changes through time (pre-, during and postlogging). The data were grouped into the four streamside treatment areas; and into six time periods; 1973–76 (prelogging), 1977–78 (post-intense treatment to November 1978 freshet), 1979–80 (post-November freshet to completion of logging), 1981–82 (postlogging period influenced by many large freshets), 1983–84 (postlogging period with only one major freshet), and 1985–86 (a period of benign flows). Data of August 1976 were included with prelogging years because only study section II could have been affected by the small 1976 clearcut in which a variable width of timber was left along the stream (Fig. 1). The November 1978 storm was used to divide the logging period because this was the first large freshet after logging commenced. Major changes in channel morphology were noted within the intense treatment area during this freshet (Toews and Moore 1982). When tests were significant, the data was separated into subgroups and the differences were explored further.

Mean particle size (Dg, Platts et al. 1979) was calculated for each layer of each core by

$$Dg = {d_1}^{w1}\cdot {d_2}^{w2}\ldots\cdot {d_n}^{wn},$$

where d = geometric mean diameter between two adjacent sieve sizes, w = proportion of the sample retained by the smaller sieve. The geometric mean between 9.55 mm and the average diameter of the largest rock was the largest diameter (d) used. It was raised to the power of the proportion of sample greater than 9.55 mm (w).

A fredle index (Fi, Lotspeich and Everest 1981) was calculated using:

$$Fi = Dg/So,$$

where $So = \sqrt{d_{75}/d_{25}}$ = the sorting coefficient, d_{75},d_{25} = particle size diameter at which 75 and 25% of the sample was finer, respectively. Fi is a single measure of the mean particle size in a sample and the associated standard deviation of the distribution of particle sizes around the mean.

Because cumulative distributions of particle sizes in the freeze-cores were lognormal, equations were used to predict the mesh size through which 75 and 25% of a sample would pass (Scrivener 1989). The least squares graphical method of Shirazi et al. (1981) was used to generate equations of the form:

$$\text{Percent} = b + a\cdot\log_{10}SIZE.$$

Where percent = inverse probability transformation of percentage of substrate smaller than a given mesh size, b = intercept of the regression line, a = slope, $SIZE$ = mesh size in millimetres.

Physical and biological data were compared through time with a correlation analysis. Annual survival to emergence for chum and coho salmon, mean lengths of emerging fry, means lengths of adult female spawners, adjusted fry lengths (fry length plus the measure of annual variability induced by egg size), peak flows during incubation, and mean Dg and Fi of the cores were related in a correlation matrix.

Four measures of mean Dg and Fi were used for each year: the mean for all samples, which included both layers from all four areas, and mean for the top layer only, mean for the bottom layer only, and mean for combined layers of areas 1 and 2. Data from areas 1 and 2 were used because their boundaries included all chum salmon that spawned above tidal influence and most coho salmon, and because they included the segments of stream that were within or downstream of the intense streamside treatment.

Results

Changes in Percent Fines

A comparison of the composition of spawning gravel within layers, streamside treatment areas, and time periods with a

TABLE 1. *F* statistics from ANOVA comparing percentage of streambed cores that were smaller than 9.55, 2.38, 1.19, 0.297, and 0.074 mm. Sample sizes and probabilities are also shown (NS = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

Analysis	Number of samples	<9.55 mm	<2.38 mm	<1.19 mm	<0.297 mm	<0.074 mm
Three-way ANOVA	1542					
Depth[a]		30.2***	53.0***	57.0***	36.3***	24.7***
Time[b]		23.2***	17.8***	13.4***	5.3***	1.0 NS
Area[c]		18.5***	13.3***	11.7***	2.3 NS	2.3 NS
Time/depth interaction		2.4*	1.1 NS	0.6 NS	0.6 NS	0.7 NS
Time/area		1.7 NS	1.6 NS	1.6 NS	1.1 NS	1.4 NS
Area/depth		0.9 NS	0.5 NS	0.8 NS	1.1 NS	1.0 NS
Two-way ANOVA (Top layer)	771					
Time		13.2***	10.5***	7.6***	4.8***	2.2 NS
Area		13.1***	9.4***	9.0***	5.6***	4.3**
Interaction		1.8*	1.6 NS	1.6 NS	2.4*	2.1*
Two-way ANOVA (Bottom layer)	771					
Time		12.3***	8.4***	6.8***	2.6*	0.7 NS
Area		6.2***	4.5**	3.6*	1.0 NS	1.5 NS
Interaction		0.5 NS	0.5 NS	0.8 NS	0.8 NS	1.2 NS

[a]Depth: (1) Top layer, (2) Bottom layer.
[b]Time periods: (1) August 1973 to August 1976, (2) September 1976 to October 1978, (3) November 1978 to December 1980, (4) January 1981 to February 1983, (5) March 1983 to August 1984, (6) October 1984 to August 1986.
[c]Areas: (1) sections II, III, and IV, (2) sections V and VI, (3) sections VII and VIII, (4) section IX.

TABLE 2. Mean percentages of 771 streambed cores that were smaller than 9.55, 2.38, 1.19, 0.297 and 0.074 mm.

Sieve size (mm)	Gravel layers (Mean % passing)		Mean increase with depth
	Top	Bottom	
9.55	32.2	35.9	3.7
2.38	12.9	15.8	2.9
1.19	6.9	8.9	2.0
0.297	1.0	1.6	0.6
0.074	0.2	0.4	0.2

three-way ANOVA indicated that there were significant differences for most particle sizes (Table 1). Only silts and clays (particles <0.074 mm) were not significantly different through time and only fine sand, silt, and clay (<0.297 and <0.074 mm) were not significantly different among areas. The greatest differences in composition were between layers in the streambed. Fines were much greater in the bottom layer of the substrate (Table 2). The changes were general throughout the data, because interaction among ANOVA cells are rare. Only interaction between depth and time was significant for particles that were smaller than 9.55 mm (Table 1).

A two-way ANOVA using data from each layer separately showed significant differences through time and among areas for all particle sizes except those smaller than 0.074 mm (Table 1). Silt and clay components (<0.074 mm) were only significantly different in the top layer of the areas. Interaction between time and area in the top layer was probably caused by differences in logging times. This was not apparent in the bottom layer of the same freeze-cores.

The nature of the differences between layers and among areas were probably caused by impacts from logging and freshets and by spatial variability. In areas 1 and 2, pea gravel and sands (particles <9.55, <2.38, <1.19, <0.297 mm) increased significantly over time in the top and bottom layers (Table 3), but their patterns were different (Fig. 2). In the top layer, the composition of these particles increased after logging or the November 1978 freshet, declined during 1981–82 (the period influenced by many large freshets) and increased again during 1983–84 and 1985–86. In the bottom layer, they increased in a stepwise manner after logging and the November 1978 freshet, but the increase was not significant until 1981–82 or 1983–84 (Table 3). Despite the similarity of patterns, the cores from area 2 contained fewer fines in both the top and bottom layers (Fig. 2). Silt and clay components (<0.074 mm) in the streambed did not change through time (Table 3). The slightly different pattern of change in area 3 appeared to be caused by the timing of streamside logging which was not begun until after the November 1978 freshet. Unlike areas 1 and 2, area 3 had no changes in the composition of the streambed until 1981–82 (Fig. 2). In the top layer, the composition of fines in all categories declined during 1981–82 (Fig. 2), but the decline was statistically significant only for pea gravel (<9.55 mm), and coarse sand (<2.38 mm), silt and clay (<0.074 mm) components. Pea gravel and coarse sand increased again in 1983–84, while fine sand, silt, and clay components did not (<0.297 and <0.074 mm, Table 3). In the bottom layer, changes through time were significant only for particles smaller than 9.55 mm. Like areas 1 and 2, no reduction in fines occurred during 1981–82, and a tendency towards increasing fines was apparent by 1983–84 (Fig. 2). Logging adjacent to area 4 produced a pattern of change that differed from the other areas. Streambed composition changed more frequently in the top layer as in the other areas, but pea gravel and sands (<9.55 mm to >0.074 mm) decreased during 1977–78 instead of 1980–81 (Table 3; Fig. 2). They had increased again by 1983–84. A freshet on February 12, 1977 (peak flow 35 $m^3 \cdot s^{-1}$) may have been responsible for this loss of fines. Its influence on areas 1 and 2 could have been masked by the intense streamside logging treatment of early 1977. The streamside of area 4 was logged during the spring of 1981 (Fig. 1), and this was the only area where fines did not decline during 1981–82. As in the other areas, pea gravel and sand composition of the bottom layer did

TABLE 3. F statistics from 1-way ANOVA comparing through time percentages of streambed cores that were smaller than 9.55, 2.38, 1.19, 0.297, and 0.074 mm. Results of paired Student-Neuman-Keul tests are shown below significant F values (NS = not significant, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$). Corresponding means are shown in Fig. 2.

Analysis	Number of samples	<9.55 mm	<2.38 mm	<1.19 mm	<0.297 mm	<0.074 mm
One-way ANOVA (Top layer)						
Area 1 Time periods	274	11.9***	10.2***	9.2***	4.7***	0.8 NS
Pair tests		6>(3 5)>(1 2 4)	6>(3 5)>(1 2 4)	(3 5 6)>(1 2 4)	(5 6)>(1 4)	
Area 2 Time periods	207	3.1*	2.9*	3.6**	3.5**	1.3 NS
		(3>4)	(3>4)	(3 2)>4		
Pair tests		(3 5 6)>(1 2 4)	(5 6)>(1 2)	(5 6)>(1 4)	(5 6)>(2 3)>4	
Area 3 Time periods	179	2.8*	2.7*	0.9 NS	1.9 NS	3.0*
		6>2>4(5>4)	1>4			
Pair tests			5>(2 4)			(1 3)>(4 5 6)
Area 4 Time periods	111	3.0*	2.4*	2.5*	2.6*	1.3 NS
		(1 5)>2	6>2		1>2	
Pair tests		6>(1 2 3 4)	(1 5)>(2 4)	(1 5)>(2 4)	5>(2 3 4)	
One-way ANOVA (Bottom layer)						
Area 1 Time periods	274	7.2***	5.5***	4.4***	2.3*	1.0 NS
Pair tests		(5 6)>4>(2 1)	(5 6)>(4 3)>2	(5 6)>(4 2 1)	(5 6)>1	
Area 2 Time periods	207	3.3**	3.6**	5.2***	2.4*	1.5 NS
Pair tests		(5 6)>(1 2)	(5 6)>(1 2 3)	6>5>(1 3)	(5 6)>(2 3 1 4)	
Area 3 Time periods	179	3.5**	1.6 NS	0.9 NS	1.0 NS	0.8 NS
Pair tests		(5 6)>(1 2)				
Area 4 Time periods	111	2.3*	1.4 NS	1.0 NS	1.8 NS	0.8 NS
Pair tests		(4 5 6)>2				

not decline, but they tended to accumulate after logging had occurred (Table 3; Fig. 2).

Since 1976, percent composition of pea gravel in the streambed increased 4.6% for areas 1 and 2 combined, while total sands (0.074–2.38 mm) increased 5.7%. Although the net increase among fines tended to be similar for the top and bottom layers (Table 4, column 3; top>bottom in area 1, bottom>top in area 2), the annual rates of change and their proportion of the percentage composition during 1973–76 were very different between layers and among particle sizes. In both areas, the annual rates of change were 1.3–1.9 times greater in the top layer for pea gravel, coarse sand, and medium sand (Table 4, column 4). Rates as a proportion of percentage composition were 1.4–3.5 times greater in the top layer than in the bottom layer (Table 4, column 5). Net increases among pea gravel and sands were similar for both layers because in the bottom layer, deposition of fines was more frequent (Fig. 2), but at a much lower rate. The net increase and rate of scouring or filling annually (Table 4, column 5) increased as the particle size decreased for both areas and layers with the exception of silt-clay. Scour and deposition rates of pea gravel and sands were inversely related to particle size and to the depth of the particles (Table 5, greater slope and intercept for the top layer). Silt and clay probably changed so rapidly that rates that were calculated from annual samples underestimated scour and deposition rates. More frequent sampling might produce better estimates for silt-clay. These rates are probably accurate estimates for pea gravel and sands because they were correlated with particle size in a semilog manner (Table 5), and because freshets were not great enough to move significant quantities of the larger particle sizes every year.

Mean Particle Size (Dg) of Gravel Cores

The pattern of change for mean Dg of each layer was similar to that found for percent fines. In areas 1 and 2, Dg changed little and inconsistently for both layers immediately after the intense logging treatment in the spring of 1977 (Fig. 3). After the November 1978 freshet, mean Dg declined during 1979–80, increased during 1981–82 and declined again during 1983–84 in the top layer of the cores (Fig. 3). In the bottom layer, it progressively declined for each time period after the November 1978 freshet. The decline was not significant until 1981–82 in area 1 ($t = -2.62, p<0.01$) and until 1983–84 in area 2 (1979–80 versus 1983–84, $t = -2.21, p = 0.028$). Logging in area 3 was not begun until the spring of 1979, and changes were not apparent until 1981–82. In the top layer, mean Dg increased in 1981–82 and declined in 1983–84 (Fig. 3). In the bottom layer, it progressively declined during 1981–82 and 1983–84. The change between 1977–78 and 1983–84 was significant ($t = -2.37, p = 0.02$). In area 4, mean Dg increased in 1977–78 prior to logging, but tended to decline thereafter (Fig. 3). The decline was significant by 1979–80 and 1981–82, in the top ($t = -1.8, p<0.07$) and bottom ($t = -2.1, p = 0.04$) layer, respectively.

Yields of Suspended Sediment

Few of the fine sediments that were deposited in streambed gravels between 1977 and 1986 were transported in suspension. Suspended sediment from the November 1978 freshet contained 36% fine sand (0.06–0.98 mm), 55% silt (0.002–0.06 mm) and 9% clay (<0.002 mm). At station B, yields of suspended sediment ranged from 11.4 to 44.5 $t \cdot km^{-2}$, but they did not increase during the periods of road construction and logging (Fig. 4). Similarly, mean sediment concentrations did not change for more than 1 yr with these activities. Maximum yield and maximum mean concentration occurred during a pre-logging water-year (1973–74), while minimums occurred during a postlogging water-year (1984–85; Fig. 4). The year of major road construction (1975–76) produced the second largest yield (33 $t \cdot km^{-2}$) at the fourth largest mean concentration, but the second smallest yield at the fourth smallest mean concentration occurred during the year following the intensive log-

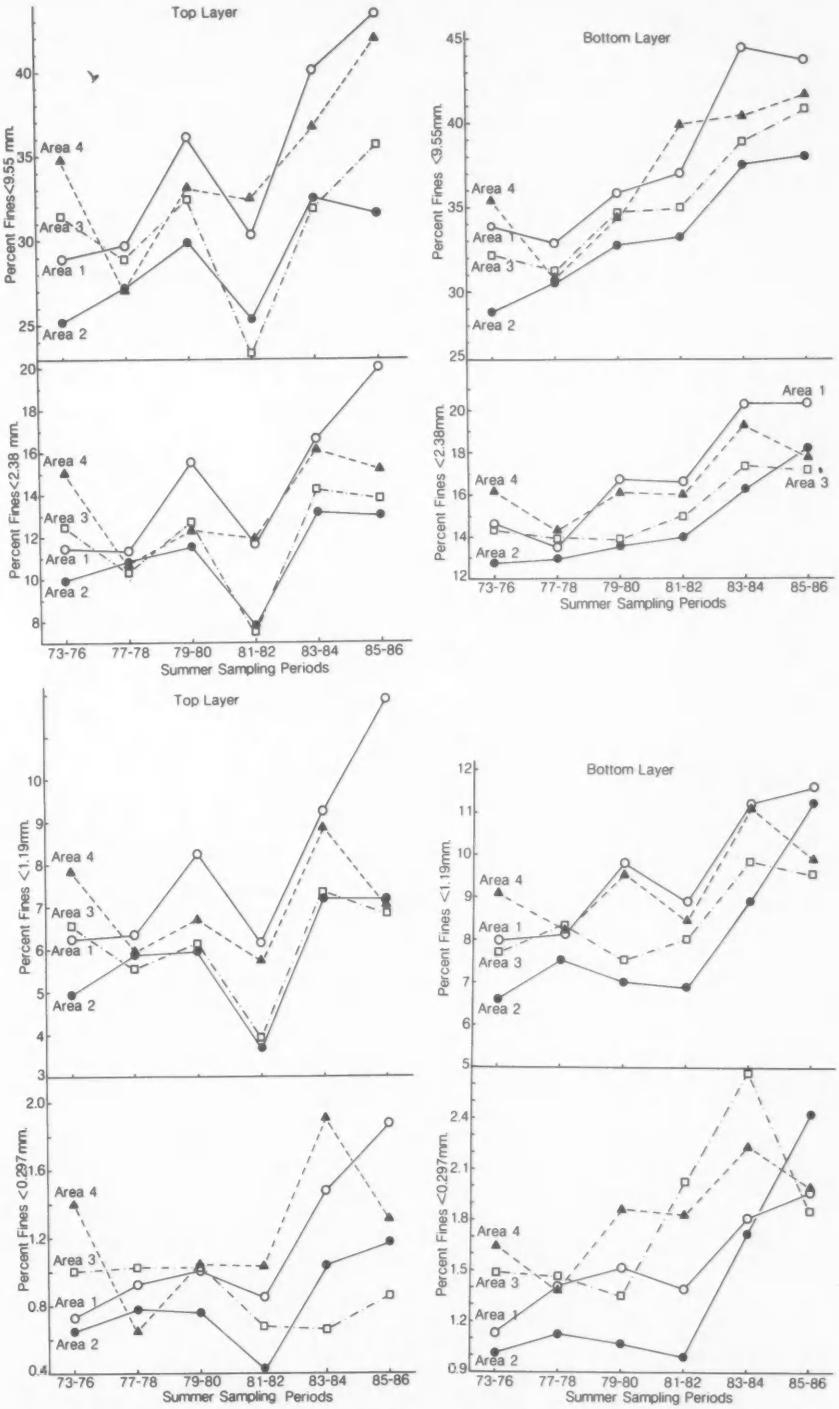

FIG. 2. Mean percentage of sample weight which passed 9.55, 2.38, 1.19, and 0.297-mm sieves. The plots include data from top and bottom layers of freeze-cores from area 1 (study sections II, III, and IV), area 2 (sections V and VI), area 3 (sections VII, and VIII), and area 4 (section IX) at Carnation Creek, British Columbia.

TABLE 4. Mean percentage composition is listed for pea gravel (2.38–9.55 mm), coarse sand (1.19–2.38 mm), medium sand (0.30–1.19 mm), fine sand (0.074–0.30 mm), and silt-clay (<0.074 mm) in streambed cores from Carnation Creek during 1973–76 (prelogging) and during 1985–86. The net increase of these fines between the two time periods (column 3 = (2–1/1)·(100%)); the annual rate of change in composition between 1973 and 1986 (sum of absolute annual changes divided by No. of years); and the proportion of annual rate of change to composition during 1973–76 are also shown.

		Column				
		1	2	3	4	5
		Composition 1973–76 (%)	Composition 1985–86 (%)	Net increase (%)	Annual rate of change 1973–1986 percent·yr^{-1}	Ratio column 4/ column 1
Area 1	Pea gravel	17.4	23.4	+34	±2.55	0.15
	Coarse sand	5.28	7.95	+50	±1.21	0.23
Top	Medium sand	5.50	10.0	+81	±1.41	0.26
layer	Fine sand	0.57	1.57	+175	±0.29	0.51
	Silt-Clay	0.16	0.22	+34	±0.04	0.25
	Pea gravel	19.3	23.8	+24	±1.65	0.08
Bottom	Coarse sand	6.50	8.60	+33	±0.91	0.14
layer	Medium sand	6.88	9.83	+43	±1.07	0.16
	Fine sand	0.86	1.72	+100	±0.27	0.31
	Silt-Clay	0.28	0.31	+11	±0.02	0.07
Area 2	Pea gravel	15.1	18.9	+25	±1.98	0.13
	Coarse sand	4.96	5.85	+18	±1.15	0.23
Top	Medium sand	4.28	6.11	+43	±1.36	0.32
layer	Fine sand	0.48	0.93	+93	±0.26	0.54
	Silt-Clay	0.17	0.29	+70	±0.05	0.30
	Pea gravel	16.2	19.6	+21	±1.51	0.09
Bottom	Coarse sand	6.03	7.36	+22	±0.63	0.10
layer	Medium sand	5.64	8.66	+53	±0.92	0.16
	Fine sand	0.78	1.76	+125	±0.26	0.33
	Silt-Clay	0.28	0.65	+132	±0.06	0.21

TABLE 5. Summary of relationships between particle size (pea gravel and sand) and the proportion of composition scouring or filling annually (from Table 4). Geometric mean diameter of pea gravel, coarse sand, medium sand, and fine sand were 4.76, 1.68, 0.57, and 0.15 mm, respectively.

	Equation	r	n	Significance
Area 1				
Top layer	Prop. = $-0.228 \cdot \text{Log}_{10}$(diameter in millimetres) + 0.278	−0.95	4	$p = 0.05$
Bottom layer	Prop. = $-0.145 \cdot \text{Log}_{10}$(diameter in millimetres) + 0.167	−0.96	4	$p < 0.05$
Area 2				
Top layer	Prop. = $-0.268 \cdot \text{Log}_{10}$(diameter in millimetres) + 0.294	−0.98	4	$p = 0.01$
Bottom layer	Prop. = $-0.161 \cdot \text{Log}_{10}$(diameter in millimetres) + 0.163	−0.93	4	$p < 0.07$

ging. Most of the particles that accumulated in the streambed were probably too large to be transported in suspension and therefore they must have been moving along the surface of the bed.

Incubation Survival of Chum and Coho Salmon

Estimates of salmon egg-to-fry survival above the counting fence declined during the study. During 1972 to 1978, survival ranged from 16.3 to 25.0% for chum salmon and from 22.5 to 37.0% for coho salmon (Fig. 5). After the November 1978 freshet, survival declined from 29.1 to 16.4% for coho salmon and from 22.2 to 11.5% for chum salmon. These changes were significant (Mann–Whitney 2 tailed U-test; chum, $p = 0.01$; coho, $p = 0.02$). An exception to the pattern occurred during 1981, when survival for chum salmon increased (Fig. 5) and when fines declined in the top layer of the streambed (Fig. 2 and 3). The intense logging treatment of area 2 in 1976–77 (some trees felled across the stream) may have directly reduced the survival of coho salmon that year, while chum salmon were not affected because they spawned below area 2 (Fig. 5). During 1985, survival of coho increased when the smallest adult returns were obtained the previous autumn (Andersen 1985), and when winter peak flows were the smallest of those observed since the November 1978 freshet. It declined again in 1986 when adult returns were also small (Andersen 1987).

Relationship Between Gravel Composition and Dissolved Oxygen

Dissolved oxygen (DO) in the streambed was positively correlated with *Dg* (Fig. 6) and *Fi* ($r = 0.40$, $p<0.01$) in the top layer, and in the total core (both $r = 0.37$, $p = 0.013$) at the 45 sites sampled in 1982. It was not correlated with either *Dg*

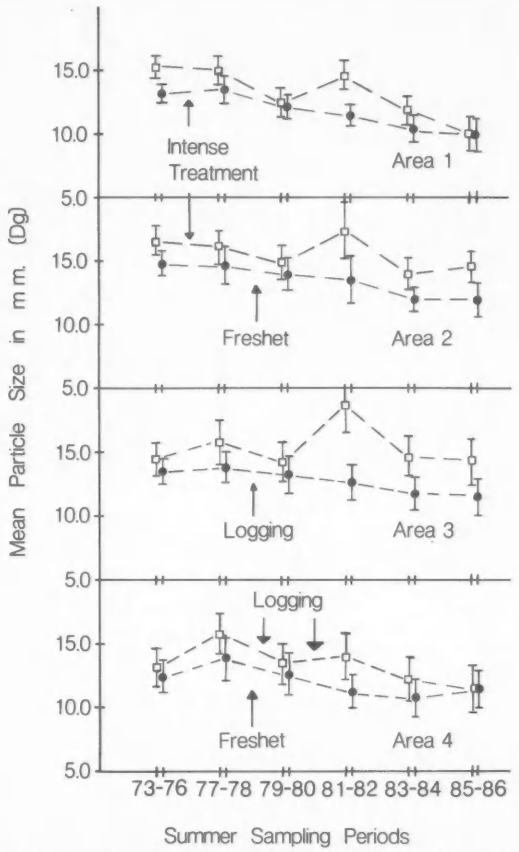

FIG. 3. Mean *Dg* (with 95% confidence limits) for top (squares) and bottom (dots) layers of streambed cores from Carnation Creek. Area 1 (downstream of the intense treatment), area 2 (intense streamside treatment), area 3 (anadromous fish habitat above this treatment), and area 4 (resident cutthroat trout habitat) include study sections II, III, and IV, sections V and VI, sections VII and VIII and section IX, respectively. Time of logging and freshets is indicated.

($r = 0.15$) or *Fi* ($r = 0.13$) in the bottom layer of the same cores. The correlations were of little value as predictive tools, because neither index of gravel quality could account for more than 20% of the variability in DO (Fig. 6). DO varied between 18 and 96% of surface concentrations when *Dg* was 10–12 mm, but it was always 60% or greater when *Dg* was more than 18 mm. Inter-gravel DO concentrations ranged from 1.3 to 8.9 $mg \cdot L^{-1}$, while they ranged from 7.5 to 9.5 $mg \cdot L^{-1}$ at the surface. Concentrations were less than or equal to 2.5 $mg \cdot L^{-1}$ at six of the 45 sites that were sampled, but these values were obtained prior to spawning during low summer flows.

Relationships Among Physical and Biological Variables

Survival to emergence of chum salmon, and fry FL and adult female FL of coho salmon decreased during the study (negative *r*, Table 6). *Dg* and *Fi* of the bottom layer and of the total core from areas 1 and 2 also declined over time. Some annual peak flows (November 16–February 15; Winter peak) have increased during the study (Table 6).

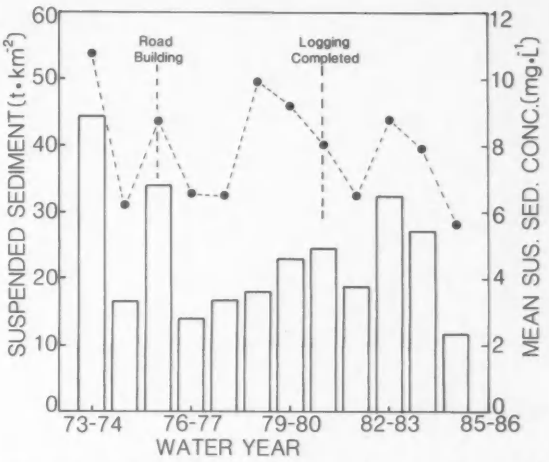

FIG. 4. Suspended sediment yield (bars) and its mean concentration (●- -●) by water-year (October to September) observed at station B in Carnation Creek watershed.

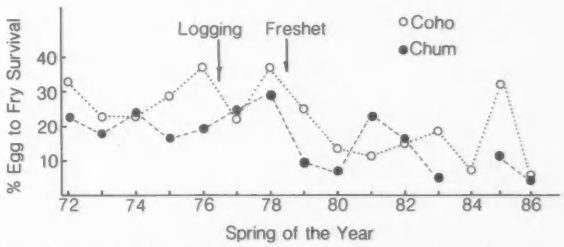

FIG. 5. Annual survival from potential egg deposition to fry emergence for coho and chum salmon located above the fish counting fence at Carnation Creek. Times of intense streamside logging during 1976–77 and the November 1978 freshet are indicated. No chum salmon females passed through the counting fence in autumn 1983.

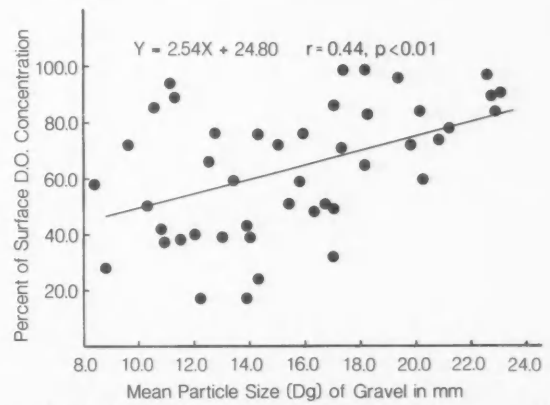

FIG. 6. Relationship between intergravel dissolved oxygen, expressed as percent of surface concentration, and mean particle size (millimetres) in the top layer of the streambed. The data were obtained from 45 Carnation Creek sites in study sections II to IX during August 1982.

Survival to emergence of chum salmon was positively correlated with *Dg* and *Fi* of the top layer of the streambed and of the two layers combined (Table 6). It was not correlated with

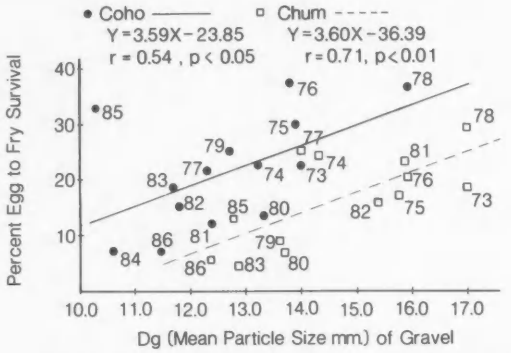

FIG. 7. Relationship between annual survival to emergence of coho salmon and mean particle size (*Dg*) in the bottom layer of freeze core samples taken from study sections II, III, IV, V, and VI; and between chum salmon survival to emergence above the counting fence and in the top layer of the same gravel cores.

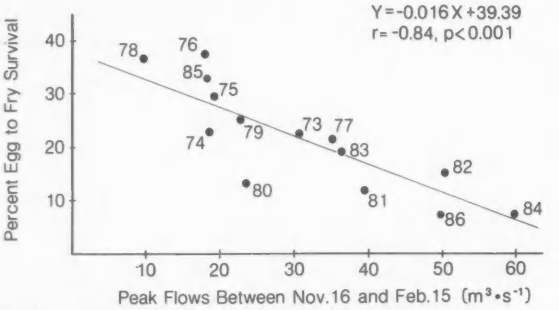

FIG. 8. Relationship between annual egg-to-fry survival of coho salmon and peak flow (B-weir) during November 16 to February 15 at Carnation Creek.

annual variations of gravel composition in the bottom layer nor with any of the peak flows. Changes of *Dg* in the top layer of the streambed explained 50% of the variability in egg-to-fry survival between 1973 and 1986 (Fig. 7). Peak survivals occurred during 1978 and 1981 (Fig. 5), when a cleaning of pea gravel and sand from the top layer was apparent (Fig. 3), but they were poor during 1979, 1980, and 1983 when intrusions of pea gravel and sand occurred. Deviations from the correlation were large and positive during 1974 and 1977, after winters of small and infrequent freshets prior to hatching (Fig. 7). A relationship between residuals and peak flows between October 20 and January 15 was not significant ($r = -0.32$, $p = 0.29$), but peak flows explained 10% of the variation of these residuals.

Survival to emergence of coho salmon was positively correlated with fry lengths, and *Dg* and *Fi* of the lower layer of the gravel cores, but it was not correlated with gravel composition in the top layer (Table 6; Fig. 7). Changes of *Dg* in the bottom layer of the streambed explained 28% of the variability in egg-to-fry survival of coho salmon. A large positive deviation from this relationship occurred during 1985 (Fig. 7), a year of very benign flows (Fig. 8). Residuals from the relationship between *Dg* and survival were correlated with peak flows between November 16 and February 15 ($r = -0.60, p = 0.02$) and they explained 36% of the variation in residuals. Egg-to-fry survival was negatively correlated with peak flows between

TABLE 6. Correlation matrix comparing chum and coho salmon annual egg-to-fry survivals; annual mean length of emerging fry, of adult females the previous autumn at the counting fence and of emerging fry corrected for egg size; annual mean particle sizes (*Dg*) and (*Fi*) of streambed gravel; and annual peek flows from Carnation Creek during 1973 to 1986 (* = $p < 0.05$, ** = $p < 0.01$).

	Year	Incubation survival: Chum	Incubation survival: Coho	Coho fry length	Coho female length	Corrected fry length	Chum fry length	Chum female length	Corrected fry length	Flow 1	Flow 2	Flow 3	Flow 4	Flow 5
Year	1.0													
Chum egg survival	−0.56*	1.0												
Coho egg survival	−0.49	0.41	1.0											
Coho fry length	−0.81**	—	0.56*	1.0										
Coho female adult length	−0.70**	—	0.36	0.72**	1.0									
Coho fry length corrected for egg size	−0.77**	—	0.55*	—	0.52	1.0								
Chum fry length	−0.20	−0.04	—	—	—	—	1.0							
Chum female adult length	0.12	−0.15	—	—	—	—	0.63*	1.0						
Chum fry length corrected for egg size	−0.41	0.25	—	—	—	—	—	0.10	1.0					
Flow 1 Peak Nov. 16 to Jan. 15	0.14	0.14	−0.45	−0.32	−0.22	−0.30	0.09	−0.36	0.44	1.0				
Flow 2 Peak Nov. 16 to Feb. 15	0.56*	−0.30	−0.84**	−0.61*	−0.47	−0.59*	0.33	0.16	0.22	0.51	1.0			
Flow 3 Peak Oct. 20 to Jan. 31	0.24	0.01	−0.39	−0.37	−0.29	−0.35	0.54	0.28	0.45	0.54	0.59*	1.0		
Flow 4 Peak Oct. 20 to Jan. 15	0.06	0.02	−0.19	−0.32	−0.17	−0.31	0.18	−0.11	0.36	0.66*	0.26	0.76**	1.0	
Flow 5 Winter Peak Oct. to Mar.	0.61*	−0.32	−0.64*	−0.59*	−0.47	−0.67*	0.50	0.30	0.09	0.33	0.87**	0.75**	0.45	1.0
Dg all areas	−0.65*	0.68*	0.50	0.76**	0.63*	0.74**	0.27	−0.27	0.64*	−0.15	−0.51	−0.05	0.02	−0.46
Dg areas 1 and 2 top layer	−0.69**	0.71**	0.46	0.80**	0.69**	0.76**	0.30	−0.29	0.71**	−0.03	−0.38	−0.03	0.00	−0.40
Dg areas 1 and 2 bottom layer	−0.75**	0.51	0.54*	0.78**	0.60*	0.79**	0.25	−0.20	0.56*	−0.32	−0.65*	−0.27	−0.11	−0.61*
Dg areas 1 and 2 both layers	−0.76**	0.65*	0.51	0.83**	0.69**	0.81**	0.30	−0.26	0.68*	−0.19	−0.54*	−0.12	−0.06	−0.52
Fi all areas	−0.40	0.57*	0.46	0.58*	0.52	0.56*	0.18	−0.27	0.51	−0.19	−0.44	−0.04	−0.03	−0.34
Fi areas 1 and 2 top layer	−0.52	0.66*	0.46	0.70**	0.60*	0.66*	0.24	−0.30	0.66*	−0.12	−0.39	0.03	−0.04	−0.35
Fi areas 1 and 2 bottom layer	−0.60*	0.49	0.53*	0.67*	0.51	0.68**	0.20	−0.17	0.48	−0.34	−0.64*	0.20	0.07	−0.55*
Fi areas 1 and 2 both layers	−0.57*	0.60*	0.50	0.71**	0.60*	0.69**	0.23	−0.27	0.60*	−0.25	−0.51	−0.09	−0.08	−0.45

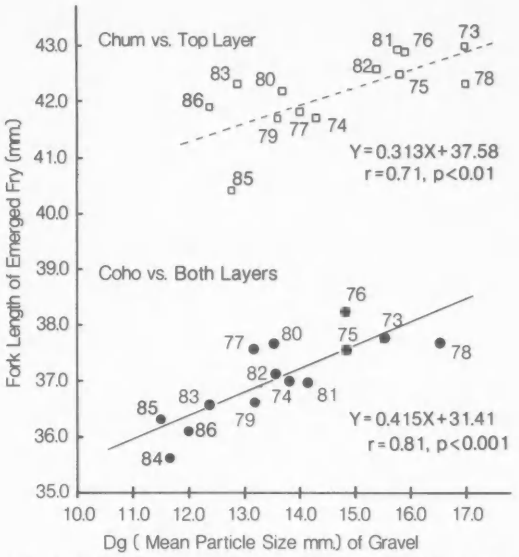

FIG. 9. Relationships between mean particle size (*Dg*) in streambed cores from study sections II, III, IV, V, and VI and the length of recently emerged salmon fry from the counting fence at Carnation Creek. Fry lengths are corrected for the influence of annual variation in size of the adult females which produced the fry.

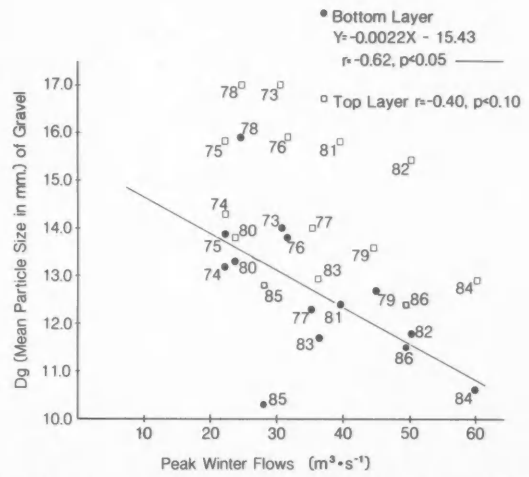

FIG. 10. Relationship between winter peak flow (the annual peak B-weir) and mean particle size (*Dg*) in the bottom and top layers of streambed cores from study sections II, III, IV, V, and VI at Carnation Creek, British Columbia.

November 16 and February 15 (Fig. 8). Peak flows and *Dg* of the lower layer of streambed cores explained 73% of the variability in incubation survival ($r = 0.86$, $r^2 = 0.73$, $p<0.001$) of coho salmon.

As expected, mean length of emerging fry of both species was positively correlated with mean FL of the adult females that produced them (Table 6), indicating that female influence on egg size was affecting fry size. After correction for variation of egg size, fry lengths of coho and chum salmon were positively correlated with *Dg* and *Fi* (Table 6; Fig. 9). The best relationship was obtained with *Dg* in the top layer for chum salmon and with *Dg* of both layers combined for coho. Length of coho fry was negatively correlated with two of the peak flow indicators (Table 6). This may reflect the fact that, fry length, and adult length of coho salmon, and gravel quality all have declined over time, while peak flows increased (Table 6). The measures of substrate composition explained more of the variability in the length of emerging coho fry than can be explained by peak flows.

Two of five indicators of peak flow were negatively correlated with substrate composition in the lower and in the combined layers of the gravel cores, but none of them were related to composition of the top layer (Table 6; Fig. 10). Fines have accumulated in the bottom layer since 1981, when greater peak flows and channel instability have been recorded. The cleaning of pea gravel and sand from the top layer during 1981 and 1982 freshets is pronounced in the scatter plot of *Dg* against annual peak flow (Fig. 10).

Discussion

Sediment Sources at Carnation Creek

In watersheds with forest harvesting, three major sources of sediment to streams are from landslides or debris torrents (Everest et al. 1987; Poulin 1986), from surface scour on logging roads (Beschta 1978; Cederholm et al. 1981), and from upstream storage (gravel bars and wedges in the stream) or erosion of the stream banks (Anderson 1971; Hartman et al. 1987). Transport of these materials occurs periodically during storms.

Since logging was begun in 1976–77, five landslides and three debris torrents in steep valley wall tributaries have occurred in Carnation Creek watershed (Hartman et al. 1987). The areas involved were small, and significant quantities of sediment from probably just one of the torrents reached the main channel. Most of the material was deposited on roads, on lower valley slopes, or on the valley floor (Hartman et al. 1987). Therefore, these sediment sources were not major contributors to the marked changes observed in the composition of spawning gravel at this time.

Road surfaces can be a major source of sediment. In the Clearwater River watershed, sediments that were washed from roads equalled the volume produced by landslides. Particles smaller than 0.85 mm in diameter in the streambed were correlated with the area of roads in the basin (Cederholm et al. 1981). Frequent heavy traffic on the roads crushed surfacing materials making them more erodable.

At Carnation Creek, roads were not a major source of the sediment that accumulated in the gravels. Roads were constructed from blasted rock and they were surfaced with hard and coarse gravel, so fines were scoured from them only during a few storms and even subsequent heavy traffic generated little sediment (Ottens and Rudd 1977). We concluded that few fine sediments from the road reached the main channel because: (1) most roads were located well away from the stream; (2) most of the sediments affecting the composition of spawning gravel were medium sands or larger (>1 mm); (3) sediments washed from road surfaces are usually finer (Cederholm et al. 1981); and (4) a small increase in the yield of suspended sediment in the main channel occurred during only one of the six years with road construction (1975–76) or logging.

In Carnation Creek, much of the sediment that affects the quality of spawning gravels probably came from scoured stream

banks or from washed channel sediments that had been protected or stored behind large organic debris (LOD) upstream. As a consequence of logging, major realignment and loss of LOD has occurred (Toews and Moore 1982), and this has greatly reduced channel and substrate stability (Everest et al. 1987). Because of the loss of living roots of streamside vegetation and because of LOD losses, greater streambank erosion has widened and straightened the channel (Toews and Moore 1982; Hartman et al. 1987), thus introducing much more material to the stream and permitting more rapid routing of sediments downstream. After logging, erosion of streambanks increased from 0.18 to 0.50 $m^3 \cdot m^{-1}$ of stream in the careful treatment area and from 0.47 to 1.25 $m^3 \cdot m^{-1}$ in the intense streamside treatment (Hartman et al. 1987). Only a slight increase occurred in the leave-strip treatment (0.37 versus 0.49 $m^3 \cdot m^{-1}$; Hartman et al. 1987). During a January 1984 freshet, loss of LOD and channel sediments in the canyon upstream of section VIII initiated a torrent which deposited materials in the careful treatment area (area 3). These sediments are being washed and redistributed downstream.

Cyclical Variations in Gravel Particle Size Distribution

Two modes of sediment transport have been described for streams: (1) suspended transport, in which fine particles are maintained in suspension by the turbulence of flowing water; and (2) bedload transport in which coarser particles (>1 mm in diameter) roll, slide, or saltate downstream in close proximity to the stream bottom. Suspended sediments increase in concentration and in particle size as stream flows increase (Maximum ≈1 mm in diameter; Everest et al. 1987). When water with its suspended load infiltrates the streambed, velocity and turbulence are reduced causing sediment to be deposited to the depth of surface water penetration. It can sift lower in the streambed if open pore spaces are available. Therefore, sediment from suspension tends to fill pore spaces in the gravel from the bottom up, leaving the upper layers relatively clean (Einstein 1968).

Suspended sediment has been the principle transport mechanism leading to reduced quality of spawning gravels in the Alsea watershed, Oregon (Beschta 1978; Adams and Beschta 1980), in the Clearwater River, Washington (Cederholm et al. 1981), and in Alaskan basins (Sheridan et al. 1984; Everest et al. 1987). The impacts occurred quite quickly and they were caused by particles smaller than 1 mm in diameter. These fines often originated from the surface of logging roads. Conversely, spawning gravels could be cleaned of these fines in as short a time as 1 yr (Adams and Beschta 1980). Annual yields of suspended sediment increased from 26–97 to 60–315 $t \cdot km^{-2}$ after road construction and forest harvesting in the Alsea watershed (Beschta 1978).

In Carnation Creek, suspended sediment did not increase after road construction or logging, and processes of suspended transport and deposition have had only a minor impact on spawning gravel. This probably occurred because soils are highly organic and contain little silt and clay (Oswald 1973), because roads were located well away from the channel, and because sediments in some tributaries were probably deposited in swampy areas when streams had to cross the valley floor to reach the main channel. Annual, postlogging transport of suspended sediment was 5 to 40% of that observed during the Alsea watershed study (Beschta 1978). The average composition was 65% silts and clays (<0.06 mm; Anon 1973–1985). These particle sizes changed so frequently in the streambed because of the many freshets that a seasonal pattern was observed during many years (Scrivener and Brownlee 1982). Spring and summer accumulations, followed by autumn and winter decreases, exceeded the net increase between 1976 and 1986 that was reported here. Changes in the composition of the streambed occurred first in the top layer which is not consistent with the processes of deposition of suspended sediments (Einstein 1968).

Given the predominance of larger materials accumulating in the gravels at Carnation Creek, sedimentation is principally by bedload transport processes. Flume studies have shown that as the various particles are moved downstream during freshets, they become trapped in the surface voids of the substrate (Beschta and Jackson 1979). The smaller the particle size the deeper they penetrate and these particles form a barrier to further intrusion (usually at ~10 cm during small freshets). The size of particles transported, the distance they move, and the depth of scour increase with increasing streamflows (Beschta and Jackson 1979). Sand particles become trapped a few centimetres below the depth to which scour occurs during a freshet. Therefore sedimentation occurs from the top down in the streambed and the composition of deeper layers is unchanged until a freshet occurs that is large enough to cause movement at considerable depths in the streambed.

Carnation Creek results showed this pattern of deposition and scour. When the volume of sands and pea gravel in the bedload was increased by watershed disturbance, changes in streambed composition became apparent first near the surface. As the stream was exposed to larger freshets with longer return periods, the depth at which sand seals were formed became greater. When the sources of sediment decline, as the basin stabilizes, and if the frequency of freshets is unchanged, cleaning of the substrate should occur in the same way, although the larger the fine particles and the deeper their penetration the slower the rate of cleaning.

Changes in gravel composition were dependent upon the frequency and magnitude of peak flows, on proximity to the different streamside treatments (sources of sediment), and on the timing of logging activities. Fines increased with gravel depth (Scrivener and Brownlee 1982), simply because cleaning at these depths was less frequent. The increase in sand and pea gravel was apparent first in the upper layers of the streambed, but eventually penetrated deeper. Sands and pea gravel were still accumulating in the deeper layers, 10 yr after logging commenced. If the new sediment sources were eliminated now (most unlikely given the instability noted; Hartman et al. 1987), the composition of the deeper layers of spawning gravel would not return to prelogging levels for another 10 yr, unless large freshets were to occur more frequently than observed over the last 16 yr (1971–1986). Upstream, fines would probably be cleaned from the top 15 cm within 3 yr should sediment sources (inchannel and streambank) be eliminated and no new sources occur, although this would also be unlikely given the instability of the channel.

Shape of streambed material can also have an appreciable effect on deposition and cleaning rates. At low flows, round gravels tended to accumulate more fine sediment than angular gravels, but this relationship is reversed as flow rates are increased (Meehan and Swanston 1977). Once fines have intruded into the streambed, cleaning is slower in angular gravels. At Carnation Creek, spawning gravels consist mainly of angular materials.

Gravel Composition and its Relationship with Other Physical and Biological Parameters

A weak correlation between gravel composition and intergravel DO was obtained from these data. Other investigators reported either a strong relationship (Koski 1975; Tagart 1984) or no relationship (Koski 1966; Scrivener and Brownlee 1982; Sowden and Power 1985). This is hardly surprising, because composition of the streambed is only one factor that effects interstitial DO. Oxygen supply to a site is a function of ambient DO and of delivery rate (Phillips 1971). Variation in ambient DO among sites was reduced for Carnation Creek data by expressing DO as a percent of surface concentration. Delivery rate (subsurface water velocity) is a function of streamflow, of hydraulic gradient, of streambed microtopography, and of flow direction over the site as well as composition of the bed (Phillips 1971; Reiser and Bjornn 1979; Sowden and Power 1985). A better correlation between gravel composition and DO may be obtained at a time when streamflow is not near summer minimums. Bed composition may have only a minor influence on interstitial DO for sites fed by upwelling groundwater instead of downwelling surface water (Sowden and Power 1985). The best relationship between DO and core composition was obtained for the top layer, because this layer effects the exchange between surface and interstitial water. All these factors should be considered if a predictive relationship is required between composition of the streambed and DO of its interstitial water.

Laboratory studies have shown that incubation survival is inversely related to gravel composition (Bjornn 1968; Phillips et al. 1975; Witzel and MacCrimmon 1981, 1983), but these results often could not be extrapolated directly to natural salmon redds (Tagart 1984; Sowden and Power 1985; Scrivener 1989). Variability of survival among redds depended on DO, on removal rates of carbon dioxide and other metabolites, on streambed scouring, and on behavioural responses of alevins as well as composition of the substrate (Koski 1966; Tagart 1984; Sowden and Power 1985). Salmonid eggs have incubated successfully in redds that contained mostly sand, but usually the fry could not escape from the substrate (Koski 1966; Tagart 1984). At Carnation Creek, this variability among redds was removed by using annual survival of the whole population and mean annual composition of the substrate. Incubating salmonid eggs require the greatest oxygen concentrations just before hatching (Alderdice et al. 1958), but alevins survive at lower DO because their gill membranes obtain oxygen more efficiently (McNeil 1966). If pore spaces in the substrate are large enough, alevins could disperse from the egg pockets (Koski 1966; Dill and Northcote 1970) and select more preferable sites (Dill 1969; Reiser and Bjornn 1979) thus reducing oxygen demand in the redd. However, fines in the substrate of some redds probably prevent this (Phillips and Koski 1969). Substrate composition influences survival indirectly during the egg incubation phase, but it has a direct effect later during any dispersal of alevins or the emergence of fry (Koski 1966; Dill 1969; Koski 1975). Emerging fry move to the surface of the bed through pore spaces in the gravel, but they can penetrate a thin layer of fine sand near the surface (Bams 1969). When these pore spaces are filled with fine sediments, fry become entombed in the bed and eventually starve to death (Phillips 1971). At Carnation Creek, entombment was probably the greatest source of mortality, because pore spaces in the substrate were filled mainly with coarse fines.

At Carnation Creek, differences of coho and chum salmon relationships between survival to emergence and composition of the streambed possibly reflected differences in redd depths between species. Coho salmon eggs were deposited at 18 to 28 cm in Oregon streams (Koski 1966). Female size was also related to nest depth among some populations of coho salmon, which indicated that most females at Carnation Creek (61 to 78 cm FL; Andersen 1983, 1984, 1985, 1987) deposited their eggs at a depth of 14.6 to 21.6 cm (depth in centimetres = 0.411·(FL cm) − 10.44; Van den Berghe and Gross 1984; Holtby and Healey 1986). This agrees with the observed relationship for coho survival and substrate composition of the bottom layer. Less information is available concerning the depth of redds of chum salmon. Eggs were deposited at 10–50 cm in Big Beef Creek, Washington and at a mean depth of 21.5 cm in Olsen Creek, Alaska (K V. Koski, National Marine Fisheries Service, Auke Bay, AK, pers. comm.). Egg deposition is probably shallower at Carnation Creek because these chum salmon produce exceptionally large eggs and because they have low energy reserves for spawning (spawn <48 h, die ~1 wk; Scrivener 1988b). Their eggs are usually found between 5 and 20 cm in December streambed cores from below the counting fence (Les Powell, Fisheries and Oceans Canada, Vancouver, B.C., pers. comm.). Many eggs are probably deposited below the top layer (>15 cm), but subsequent scour leave them at shallower depths during most of the period of incubation. Therefore incubation survival of chum salmon related better to composition of the top layer of streambed cores.

During other studies, deposition of fines in the streambed has caused size selective mortalities among large fry that were emerging from salmon redds (Koski 1966, 1975; Tagart 1984; Sowden and Power 1985). Differences of morphology such as cranial diameter among species have also been cited as the reason for survival differences in laboratory experiments using various incubation mixtures of gravel (Phillips et al. 1975; Reiser and Bjornn 1979; Witzel and MacCrimmon 1983). At Carnation Creek, increasing fines were correlated with declining sizes within the total population of emerging coho fry but the relationship was not apparent for chum salmon until the influence of egg and female size on size of progeny was removed statistically. Variability of female and egg sizes also masked size selective mortality among emerging fry of chum salmon at Big Beef Creek (Koski 1975). Selection against larger fry would alter the relative fitness of coho rearing in a stream or chum salmon emigrating to the ocean. Shortly after emergence, both species are subjected to intensive mortalities that are selective against the smaller sizes (Chapman 1966; Healey 1982). This has apparently reduced survival among returning adults of Carnation Creek chum salmon (Scrivener 1988b).

Emerging chum salmon fry were larger than those of coho salmon. This difference might also explain why the size and survival of chum salmon fry were better correlated with streambed composition in the top layer, while fry size and survival of coho salmon were better correlated with the composition of the bottom layer. Mean FL of chum salmon fry was 41.8 mm (Scrivener 1988b), while mean FL of emerging coho fry was 37.1 mm (Andersen 1983, 1984, 1985, 1987) during 1972 to 1986. The larger chum fry probably had greater difficulty penetrating the top layer of the substrate with its more variable fines than the smaller coho salmon fry.

Peak flows can influence survival of incubating eggs and alevins through changes in the stability of spawning gravels (McNeil 1966), or when they are linked with changes in com-

position of the bed as reported here (Fig. 10). Stability of the bed has declined at Carnation Creek as indicated by changes in channel morphology and in stability of LOD (Toews and Moore 1982; Hartman et al. 1987). These factors are reflected in the strong relationship between coho survival to emergence and peak flows. The weak relationship between peak flows and survival of chum salmon was obtained because chum redds were probably shallower than coho redds. Therefore, a threshold of maximum potential impact on chum salmon could be occurring more frequently and at much smaller peak flows (see Fig. 8). The fact that significant relationships were obtained between peak flows and streambed composition of the bottom, but not the top layer supported this hypothesis. Changes were so common for the top layer that more frequent sampling would be required to directly relate streamflow to either substrate composition in the top layer or incubation survival of chum salmon.

The positive relationships between composition of the streambed and peak flows should deteriorate and they could become inverse relationships as sources of new sediments decline and the cleaning of fines is begun. The positive relationship developed because large freshets scoured fines from the stream banks and distributed them in the bed. That was the habitat degradation stage being observed. During the rehabilitation stage, large freshets should be related to the scouring of fines from the streambed and their transport to the estuary. Data from 1985 to 1986 appeared to weaken the relationships between composition of the streambed and peak flows (see Fig. 10) indicating that Carnation Creek could be entering either a stage of equilibrium between deposition and scour or that after a decade the rehabilitation stage was about to begin.

Planning and Management Implications for Coastal Forest Harvesting Operations

The transfer of Carnation Creek results to resource managers has been the focus of countless presentations both on site and in various lectures, workshops (Hartman 1982; Chamberlin 1988), and conferences (Hartman et al. 1987; Holtby et al. 1984). In their development, the new fishery forestry guidelines that are now being implemented for forest harvesting throughout coastal British Columbia have drawn largely upon Carnation Creek results and our understanding of watershed processes (BCMFL et al. 1987).

It is very clear that gravel composition and stability are closely tied to the integrity of the riparian zone and to LOD in the stream (Hartman et al. 1987; Bisson et al. 1987). Forest management practices that had the greatest destabilizing influence in this area were streamside felling and yarding activities (Toews and Moore 1982). Specific impacts that must be considered include direct physical damage, exposure of the banks, and loss of living root networks due to these activities. In active fluvial floodplains, living roots have a major role of maintaining the stability of streamside zones (Sullivan et al. 1987). These observations have held true for many other streams including the Eve River, Nimpkish River, and Kim Creek in British Columbia (D. Morrison, B.C. Ministry of Environment, Nanaimo, pers. comm.). Damage to LOD by felling and yarding or the introduction of smaller pieces that lodge behind stable instream structures, that create dams, and that subsequently initiate undercutting or sidecutting must also be avoided. Smaller debris that is unstable can also be transported by the stream to more sensitive zones downstream. Streamside practices that directly impact on these riparian or instream features or indirectly by accelerating windthrow must be carefully planned in order to avoid these consequences. Consideration to the long-term source of LOD, particularly larger growing conifers (Bisson et al. 1987; Hartman et al. 1987; Poulin 1986) must also be given consideration now, if stream channel complexity and stability are to be maintained throughout the forest harvesting rotation. Forestry activities in riparian zones that are adjacent to salmonid habitat should be reduced and strips of timber left where stream waters have enough energy to cause considerable erosion or to transport large volumes of sediments and LOD. These leave strips should not be fixed in size, but tailored to each specific stream side and watershed geology.

In addition, opportunities for resource managers to offset or mitigate these impacts are becoming more apparent. Placement of armoring materials on destabilized banks, placement of LOD in channels to stabilize bedload (Hartman and Scrivener 1986), promotion of deciduous brush and tree species to stabilize stream banks (Sullivan et al. 1987), enhancement of off-channel habitat for rearing if instream areas are inhospitable during freshets (Cederholm and Reid 1987) are examples. Resource managers must give these opportunities more careful consideration. The new fishery forestry guidelines for coastal British Columbia reflect these results and permit exploration of these opportunities (BCMFL et al. 1987).

Resource managers must understand fluvial processes in a watershed in order to develop the best forest harvesting plan. Increased mortality among incubating salmon eggs was reported during the Clearwater (Cederholm et al. 1981; Tagart 1984) and Carnation Creek watershed studies. This was also implied for the Alsea watershed and Queen Charlotte Island studies, when the quality of spawning gravel declined (Moring 1975; Poulin 1986), but the size of offending particles in the streambed, their mode of transport and deposition, and their source areas varied among the studies. Therefore, the required management prescriptions to reduce incubation mortalities may have to be specific to given areas and to those problems identified.

The duration of impacts must also be considered by managers if the best resource options are to be chosen and long-term problems alleviated. For example, silt and clay size particles may produce impacts of shorter term that might be less harmful than longer term sedimentation of larger particles. The duration of impacts may be also influenced by their magnitude. If these impacts are of long duration, then the cumulative effect from some natural occurring regulators are more probable. Events that are natural and detrimental such as floods in the stream or El Nino currents in the ocean can act synergistically with these man-induced impacts to severely affect the resilience of a salmon stock (Cederholm et al. 1981; Holtby 1988; Scrivener 1988b).

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Mono- and Duoculture of Juvenile Atlantic Salmon (*Salmo salar*) and Arctic Char (*Salvelinus alpinus*)

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In a duoculture experiment with Atlantic salmon parr (*Salmo salar*) and two Arctic char (*Salvelinus alpinus*) strains, both species showed increased growth rates compared with monoculture. In duoculture, salmon dispersed more evenly than in monoculture, maintaining positions among the char. Less frequent occurrence of dorsal fin rot was observed in duoculture salmon, probably indicating decreased intraspecific aggression, compared with monoculture salmon. It is suggested that shading and increased dispersion allowed a decrease in intraspecific salmon aggression. Arctic char social hierarchy, indicated by variance of mean inter-renal cell nucleus area, was changed in the presence of salmon, favouring the largest individuals belonging to one of the strains. Different ecological adaptations and size differences can explain the difference in growth gain from duoculture between the char strains. Temperature is suggested as a behavioural regulator in salmon–char duoculture.

Une expérience de duoculture de tacons de saumons de l'Atlantique (*Salmo salar*) et de deux souches d'omble chevalier (*Salvelinus alpinus*), a permis de montrer que ces espèces présentaient des taux de croissance accrus par rapport à ce qui se passait en monoculture. Ainsi, en duoculture, les saumons se dispersaient plus régulièrement, restant parmi les ombles. De plus, la pourriture de la nageoire dorsale du saumon était moins fréquente en duoculture qu'en monoculture, indiquant probablement ainsi une agression intraspécifique moindre. D'après les auteurs, l'ombre et la dispersion accrue pourraient expliquer la diminution de l'agression intraspécifique des saumons. La hiérarchie sociale de l'omble chevalier, indiquée par une variation de la superficie des noyaux de cellules interrénales, a été modifiée par la présence des saumons; la hiérarchie favoriserait les individus les plus gros de l'une des deux souches. Diverses adaptations écologiques des différences de taille peuvent expliquer les différences d'augmentation de croissance entre les souches d'omble en duoculture. La température serait peut-être un régulateur de comportement dans la duoculture de saumon et d'omble.

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The value to producers of salmonids cultured in Norway was approximately $362 000 000 U.S. in 1987. Salmonid culture, mainly *Salmo salar*, contributed 23.5 % of the total Norwegian fish export value. However, the production is far from achieving maximum cost effectiveness (e.g. Hansen and Holm 1987), therefore even small improvements will yield considerable economic gains. Studies of fish behaviour may lead to improved cost effectiveness of aquaculture production (Riedel 1973).

In his classic paper, Kalleberg (1958) states that in intensive rearing of territorial salmonids, population densities are higher than under natural conditions. Every pisciculturist knows that in rearing troughs the fry do not as a rule exhibit any territoriality. Instead, there is a tendency towards schooling. Keenleyside and Yamamoto (1962) found in their density experiments that dominants were less likely to attack when they were schooling, because of the tendency of subdominants to flee and disappear into the school. But aggression still exists under high densities (e.g. Abbott and Dill 1985; Fernö and Holm 1986), and should be considered as a negative factor in salmonid culture.

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Polyculture, decreasing the density of each species, may be effective in regulating fish aggression. According to Yashouv (1968), ecologically different species will not compete when food is in surplus. Inter- and intraspecific competition will increase when density exceeds food resources. There may also be different ecological adaptations among populations within a species which to some extent may provide similar effects. Under natural conditions, species live sympatrically. Even mixed-species schools of fishes in the sea have been reported (Eibl-Eibesfeldt 1955; Breder 1959; Shaw 1970; Ehrlich and Ehrlich 1973).

Atlantic salmon (*Salmo salar*), brown trout (*S. trutta*), and/or Arctic char (*Salvelinus alpinus*) have a sympatric distribution in many river and lake systems. According to Mork (1977) and Nortvedt and Holm (1988), salmon may show mainly interspecific aggression, under certain duoculture conditions, while char practice more intraspecific aggression. A positive gain for salmon in duoculture should therefore be expected. In addition to the fact that large dominants tend to express agonistic behaviour towards smaller subdominants (Symons 1968; Noakes 1980), aggression in salmonids seems to be high between fish of the same size (Newman 1956; Symons 1968; Fernö and Holm 1986). Arctic char attack conspecifics partly on their ventral side, which is rare in salmonids. Small individuals of char were

often more aggressive in duoculture than larger ones (Mork 1977).

The present study investigates whether possible changes in competition due to culture type can be detected in a parameter characterizing social stress (e.g. mean nucleus size in interrenal cells) or in growth rate. A more practical intention of the study was to learn more about the potential of mixed species in aquaculture. To this end, duoculture and monoculture groups were reared experimentally. In the char groups, both duo- and monoculture, a mix of two allopatric strains was used to give an indication of the generality of the results.

Material and Methods

The experiment was carried out at the Matre Aquaculture Station (Institute of Marine Research) from 25 September 1986 (Day 1) to 06 February 1987 (Day 135). The experiment was conducted in six dark green, covered circular fibreglass tanks, 1.5 m in diameter, with bottoms sloping slightly to a vertical center sieve. Water depth was 80 cm, and volume about 1400 L.

Water Quality

Water temperature was recorded daily (Fig 1). Three periods of temperature could be distinguished. Mean temperature Day 1–43 (period I) was 12.3°C. Between Day 44 and 83 (period II) the temperature fell, giving a mean of 6.6°C. In the last period (period III; day 84–135) it was more stable with a mean value of 7.8°C, but fluctuated more near the end. Water pH varied between 5.8 and 7.3

Fish

Atlantic salmon fingerlings (0+ yr) of mixed genetic origin from Matre Aquaculture Station were used. Mean fork length at start of the experiment was 75.7 mm (SD = 9.48 mm), and mean weight was 5.8 g (SD = 2.33 g).

Arctic char fingerlings (0+ yr) consisted of two defined strains. Hammerfest (anadromous, northern) and Skogseid (landlocked, southern) strains were used in a proportion of 0.309 : 1.000. Fish of the Hammerfest strain had an initial mean fork length of 92.5 mm (SD = 12.0 mm) and weight of 9.3 g (SD = 3.66 g). Initial mean fork length at start in the Skogseid strain was 77.1 mm (SD = 12.7 mm) and mean weight was 5.2 g (SD = 2.65). The Hammerfest char were fin clipped (adipose fin).

Experimental Design

The experiment consisted of three groups, each with two replicate tanks. The set-up is outlined in Table 1. The groups were salmon in monoculture (MS1 and MS2), char in monoculture (MC1 and MC2) and salmon together with char in duoculture (DS1, DS2, and DC1, DC2, respectively).

Initial fish density was 11.7–12.6 $kg \cdot m^{-3}$. At termination of the experiment, maximum fish density was 125.3 $kg \cdot m^{-3}$ (MC2) and minimum density was 52.5 $kg \cdot m^{-3}$ (MS1).

The fish were exposed to 24-h light from 60 W light bulbs, placed 30 cm above the surface of each tank. They were fed dry feed by AQUAPRODUKTER (TM) automatic feeders every 10 min with calculated rations, for salmon as recommended by Austreng et al. (1987). Calculated rations for char were as recommended by Jobling (1983) and modified according to previous char rearing experience at Matre Aquaculture Station.

Sampling, Measurements, and Histology

Water level in the tanks was lowered to diminish size-dependent avoidance, when sampling fish to measure length and weight. Sampled fish were anaesthetized with benzocaine. At least 90 salmon and 100 char from each tank were measured each time. All individuals in some tanks were weighed, to ensure that there was no size-bias when sampling. Measurements were made on Day 1, 43, 83, and 135.

Blood was sampled on Day 77 (in period II). Standard sampling technique (puncture of caudal vein) was used with heparin treated needles. PCV (Packed cell volume) and leucocrit were measured after centrifuging at 2000 rpm for 10 min at 15°C.

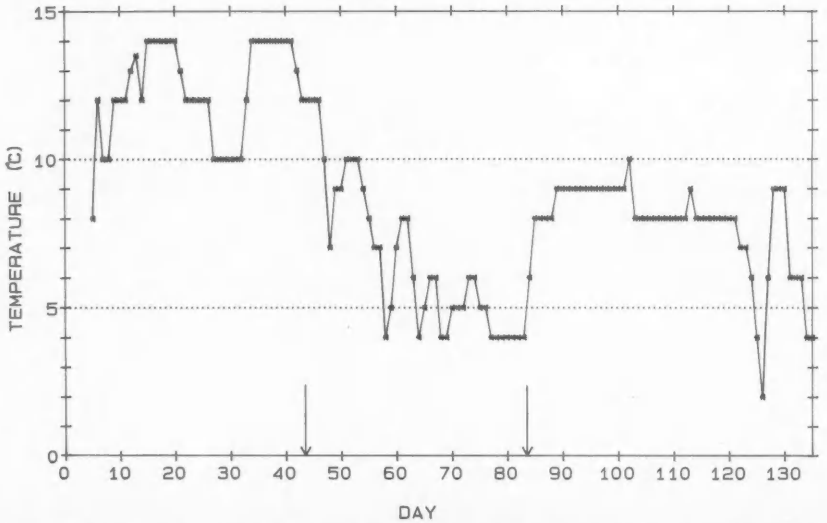

FIG. 1. Water temperature measured in the experimental tanks. Arrows on the time axis indicate the three periods.

TABLE 1. Initial and final numbers and intervening losses due to sampling and mortality in salmon and char, in each replicated group, when cultured alone (monoculture) or together (duoculture).

	Monoculture				Duoculture			
	MS1	MS2	MC1	MC2	DS1	DC1	DS2	DC2
Initial No. (Day 1)	2890	2890	2890[a]	2890[a]	1446	1446[b]	1446	1446[b]
Removed for sampling	20	20	20	20	20	20	20	20
Observed mortality	58	67	181	132	38	94	36	61
Observed loss due to technical accident	0	0	0	0	18	0	3	21
Unrecorded loss	0	11	36	27	1	0	6	0
Final No. (Day 135)	2812	2792	2653	2711	1369	1332	1387	1344
Observed mortality and unrecorded loss as percent of initial No.	2.0	2.7	8.2	5.5	2.7	6.5	2.5	5.7

[b]Consisting of 241 Hammerfest and 1105 Skogseid strain.
[a]Consisting of 681 Hammerfest and 2209 Skogseid strain.

Head kidneys were sampled from the same fish on Day 77, fixed, embedded, and stained as described in Holm (1989). The sections were analyzed on an Ernst–Leitz–Wetzlar ASM 68 K (TM) semiautomatic image analysis system, using a 64 × ocular. Inter-renal nuclear area (square micrometres) was measured without being aware of sample origin. A minimum of 25 nuclei from three to five cell groups were examined from each fish (Donaldson et al. 1984).

Formulae and Statistics

Fultons condition factor (K) was calculated as:

$$K = 100 \cdot W \cdot FL^{-3},$$

where W is individual fish weight (grams) and FL is individual fish fork length (centimetres).

Fork length increase (FLI) was calculated for a group of fish as:

$$FLI = (FL_B - FL_A) \cdot (\Delta t \cdot T)^{-1} \qquad (\text{mm} \cdot \text{d}^{-1} \cdot {}^{0}\text{C}^{-1}),$$

where FL_A is mean fork length at Day A, FL_B is mean fork length at Day B, Δt is number of days between Day A and Day B, T is mean temperature in period Day A–Day B.

Specific growth rate (SGR) was calculated for a group of fish according to Houde and Schekter (1981) as:

$$SGR = 100 \cdot (e^{C} - 1) \qquad (\%\ \text{weight increase} \cdot \text{d}^{-1}),$$

where $c = (\ln W_B - \ln W_A) \cdot \Delta t^{-1}$,

where W_A is mean weight at Day A, W_B is mean weight at Day B, other parameters as above.

Coefficient of variation (CV) was calculated as:

$$CV = \text{SD} \cdot 100 \cdot X^{-1} \qquad (\%),$$

where SD is standard deviation to X, and X is FL or W.

Fork length, weight, and condition factor were analyzed in a factorial two-way ANOVA (culture type, species), according to Sokal and Rohlf (1981).

A Fisher–Irwin test for 2 × 2 tables (Hodges and Lehmann 1975) was used for testing for equality in survival between tanks within species, and equality in incidence of dorsal fin rot (infection present caused by lately biting injuries) between tanks in salmon, both at Day 135.

A Kolmogorov–Smirnov test for normality was used for all length and weight samples. If one or two samples were non-normally distributed, Ansari–Bradley's test for equality of dispersions was used before Mann–Whitney's test for pooled samples with equal dispersions.

If both samples were normally distributed, F-test for equality of variance was used before t-test with pooled or unpooled variance. Blood parameter values were also tested this way, except for the leucocrit values which were arcsin transformed before t-testing (Sokal and Rohlf 1981). A single classification ANOVA (Sokal and Rohlf 1981) was also used for testing differences between treatments in blood parameters. All statistical tests, except the single classification ANOVA and Fisher–Irwin test, were carried out on the computer-based data analysis system RS/1 (TM) (Anon 1983).

Results

Arctic char dispersed homogenously in the water column in both mono and duoculture. Atlantic salmon in monoculture tended to stay in clusters near the tank bottom. In duoculture, the salmon dispersed more evenly, positioning among the char. This phenomenon was observed during the entire experimental period.

Mortality

Mortality in salmon did not exceed 2.7% (Table 1). The char showed higher mortality, up to 8.2%. Except for DC1, the highest mortality in char was observed in the Hammerfest strain. Some of the mortality was probably partly due to fluctuations in pH. Mortality episodes were observed concurrently with pH-related mortality in sensitive salmon groups elsewhere at the Matre Aquaculture Station. There no significant differences in mortality between either replicates or treatments (Fisher–Irwin, $p > 0.05$).

Variation in Size Parameters

In general, both culture type and species contributed significantly to the variation in fork length, weight, and condition factor at end of all three periods (except for weight versus culture type on Day 43; Table 2). For length and weight, interaction effect was declining from highly significant on Day 43 to non-significant at termination. The variation in condition factor was significantly affected by the interaction effect throughout the entire experiment.

Growth Rate in Atlantic Salmon

On Day 83, the difference in mean fork length (FL) of salmon in mono- and duoculture was significant (Table 3). On Day 43

TABLE 2. Factorial two-way ANOVA of size parameters (PAR) versus culture type and species. d.f. = degrees of freedom, SS = sum of squares. Asterisk indicates $0.01<p<0.05$; Double asterisk indicates $p<0.01$; ns = not significant; C = char; S = Salmon.

	DAY 43		DAY 83		DAY 135	
	d.f.	SS	d.f.	SS	d.f.	SS
PAR: Length						
Culture type	1	1661.40*	1	25 469.75**	1	3 917.06**
Species	1	16 549.06**	1	49 892.62**	1	383 136.99**
Interaction C·S	1	14 588.69**	1	788.07^{ns}	1	2 045.19^{ns}
Error	1308	480 924.62	1274	607 108.67	1390	845 820.05
PAR: Weight						
Cutlure type	1	91.25^{ns}	1	13 099.62**	1	4 698.57**
Species	1	2 473.37**	1	23 076.19**	1	381 658.51**
Interaction C·S	1	2 813.36**	1	1 042.61*	1	165.69^{ns}
Error	1308	96 252.07	1274	257 240.55	1390	852 178.56
PAR: Condition factor						
Culture type	1	0.147**	1	0.353**	1	0.047*
Species	1	5.082**	1	0.489**	1	2.586**
Interaction C·S	1	0.085*	1	0.061**	1	0.068**
Error	1308	18.151	1274	10.456	1390	12.613

TABLE 3. Atlantic salmon fork length and growth rate. *FL* = mean fork length (mm), *FLI* = fork length increase ($mm \cdot d^{-1} \cdot °C^{-1}$), Max *SGR* = maximum *SGR* according to Austreng et al. (1987), Obs *SGR* = observed specific growth rate (% weight increase·d^{-1}). *FL* values marked with different letters at same date are significantly different (*t*-test, $p<0.05$).

		Experimental group			
Parameter	Time	DS1	DS2	MS1	MS2
			75.7		
FL	Day 1				
	43	109.7^a	115.8^b	108.0^a	105.5^a
	83	125.6^a	125.6^a	120.0^b	119.1^b
	135	133.8*^{a}	140.1^b	131.9^a	133.0^a
FLI	Period I	0.066	0.078	0.063	0.058
	II	0.060	0.037	0.045	0.052
	III	0.020*	0.036	0.029	0.034
Max *SGR*	Period I	2.7	2.7	2.7	2.7
	II	1.0	1.0	1.0	1.0
	III	1.2	1.2	1.2	1.2
Obs *SGR*	Period I	2.62	2.84	2.40	2.37
	II	0.89	0.69	0.71	0.72
	III	0.25*	0.55	0.48	0.54

*Water circulation problems in DS1 in period III.

and 135, one of the duoculture groups (DS2) had significantly higher lengths than the three other groups. Coefficient of variation (*CV*) at Day 135 was 14.2% in the duoculture salmon and 12.1% in monoculture, and variance was significantly larger in duoculture than in monoculture salmon (*F*-test, $p = 0.0002$).

At the end of period II (Day 83), there was no difference between replicates, but a significant difference between culture types (Fig. 2A). Salmon in duoculture were on average 18.7% heavier than the salmon in monoculture. At Day 135, the DS2 group was significantly larger than the three others. CV at Day 135 was 38.3% in duoculture, and 30.0% in monoculture. The variance was significantly greater in duoculture (*F*-test, $p = 0.0002$).

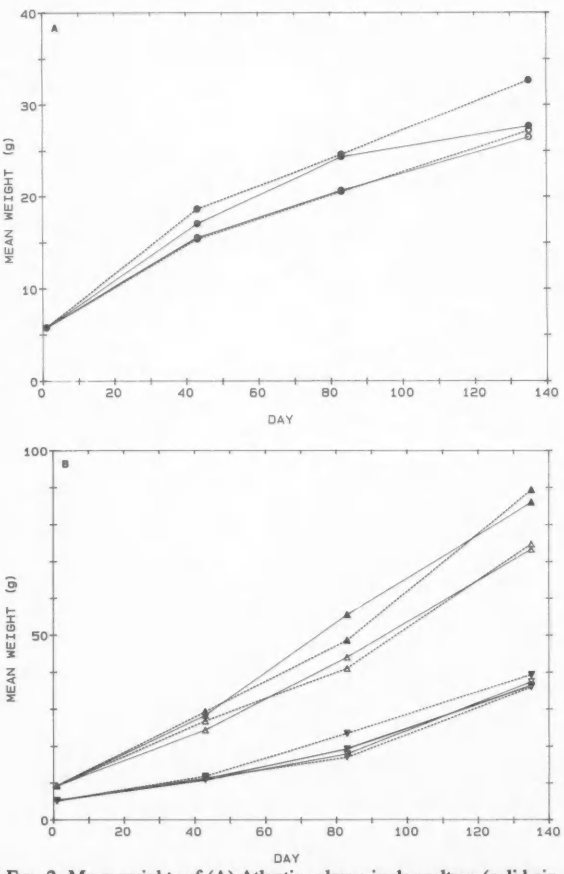

FIG. 2. Mean weights of (A) Atlantic salmon in duoculture (solid circles) and in monoculture (open circles), and of (B) Hammerfest char (triangles) and Skogseid char (inverse triangles) from the beginning to end of the experiment. Line type differentiates between the replicates.

TABLE 4. Arctic char (Hammerfest strain) fork length and growth rate. *FL* = mean fork length (mm), *FLI* = fork length increase ($mm \cdot d^{-1} \cdot °C^{-1}$), Max *SGR* = maximum SGR according to Jobling (1983), Obs *SGR* = observed specific growth rate (% weight increase$\cdot d^{-1}$). *FL* values marked with different letters at same date are significantly different (*t*-test, $p<0.05$).

Parameter	Time		Experimental group			
			DC1	DC2	MC1	MC2
FL	Day	1	92.5			
		43	129.8[a]	132.4[a]	127.3[a]	126.7[a]
		83	164.5[a]	158.0[b]	152.9[c]	151.8[c]
		135	189.4[a]*	189.4[a]	180.1[b]	182.2[b]
FLI	Period	I	0.072	0.077	0.067	0.066
		II	0.131	0.097	0.097	0.095
		III	0.061*	0.077	0.067	0.075
Max *SGR*	Period	I	3.33	3.33	3.33	3.33
		II	1.27	1.26	1.33	1.29
		III	1.20	1.25	1.29	1.32
Obs *SGR*	Period	I	2.71	2.78	2.33	2.57
		II	1.69	1.27	1.49	1.07
		III	0.84*	1.18	0.99	1.20

*Water circulation problems in DC1 in period III.

TABLE 5. Arctic char (Skogseid strain), fork length, and growth rate. *FL* = mean fork length (mm), *FLI* = fork length increase ($mm \cdot d^{-1} \cdot °C^{-1}$), Obs *SGR* = observed specific growth rate (% weight increase$\cdot d^{-1}$). *FL* values marked with different letters at same date are significantly different (*t*-test, $p<0.05$).

Parameter	Time		Experimental group			
			DC1	DC2	MC1	MC2
FL	Day	1	77.1			
		43	99.1[a]	100.8[a]	96.8[a]	100.2[a]
		83	116.6[a]	124.9[b]	114.3[a]	114.4[a]
		135	144.0[a]*	147.0[a]	144.5[a]	142.9[a]
FLI	Period	I	0.043	0.048	0.038	0.045
		II	0.066	0.091	0.066	0.054
		III	0.068*	0.054	0.074	0.070
Obs *SGR*	Period	I	1.85	2.00	1.77	1.89
		II	1.38	1.72	1.28	1.02
		III	1.23*	1.00	1.42	1.45

*Water circulation problems in DC1 in period III.

For period I, observed growth (*SGR*) was close to the maximum (91–105% of expected according to Austreng et al (1987), Table 3). For the two cold water periods, observed growth rate was lower than expected (period II: 69–89% of exp., period III: 21–46%). There were no differences in *K* at Day 135 ($K = 1.10$ for both culture types).

Growth Rate in Arctic Char

At the end of period II (Day 83), Hammerfest char in DC1 were significantly larger than in DC2, and both duoculture groups were significantly larger than the monoculture groups (Table 4). At the end of period III (Day 135), there was no difference between replicates, although the duoculture fish were still significantly larger than the monoculture fish, and the relative difference had decreased. CV was almost identical for the two culture types, and there was no significant difference in *FL* variance.

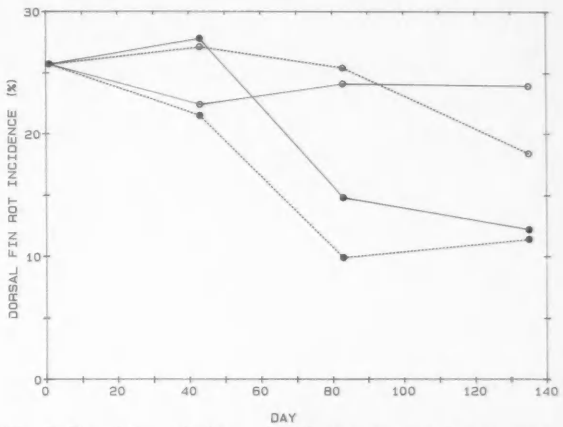

FIG. 3. Dorsal fin rot incidence in Atlantic salmon during the experiment. Symbols as in Fig. 2A.

TABLE 6. Packed cell volume (PCV), leucocrit, and plasma chloride on Day 77 from char and salmon blood. Each table cell refers to mean of 10 individuals. Standard deviation in parentheses. Significant differences ($p<0.05$) between replicates are indicated by an asterisk, leucocrit values were arcsin transformed before testing.

Experimental group	PCV (%)	Leucocrit (%)	Plasma chloride (milliMolar)
MS1	43.9 (3.9)	0.30 (0.09)	112.3 (2.6)
MS2	37.2 (5.9)*	0.46 (0.17)*	127.9 (4.1)*
DS1	46.1 (11.0)	0.15 (0.04)	120.0 (11.7)
DS2	40.3 (5.4)	0.36 (0.12)*	125.3 (6.4)
DC1	47.8 (8.4)	0.12 (0.03)	108.6 (11.7)
DC2	45.4 (4.3)	0.37 (0.08)*	121.7 (5.0)*
MC1	48.9 (8.5)	0.30 (0.23)	114.0 (7.5)
MC2	47.4 (2.7)	0.27 (0.08)	122.6 (7.3)*

The differences between mean weights on Days 83 and 135 were similar to those for mean lengths (Fig. 2B). At Day 135, Hammerfest char in duoculture were on average 18.4% larger than the monoculture fish. *CV* was 33.1% in duoculture and 33.2% in monoculture; the variance was significantly larger in duoculture (*F*-test, $p = 0.021$).

Observed *SGR* was 70–83% of the expected (Jobling 1983) in period I, 83–133% in period II and 70–94% in period III (Table 4). Mean *K* in duoculture at Day 135 was 1.24, which is significantly higher than 1.19 in monoculture (*t*-test, $p<0.05$).

The DC2 fish were significantly larger in fork length than the others on Day 83, but no other significant differences were found (Table 5). CV was 12.6% in duoculture and 14.6% in monoculture; the variance was significantly larger in monoculture (*F*-test, $p = 0.033$).

The differences in mean weights were the same as for mean lengths (Fig 2B). *CV* in duoculture was 39.8 and 45.7% in monoculture. The variance of *W* was slightly larger for monoculture (*F*-test, $p = 0.072$). The condition factor in duoculture

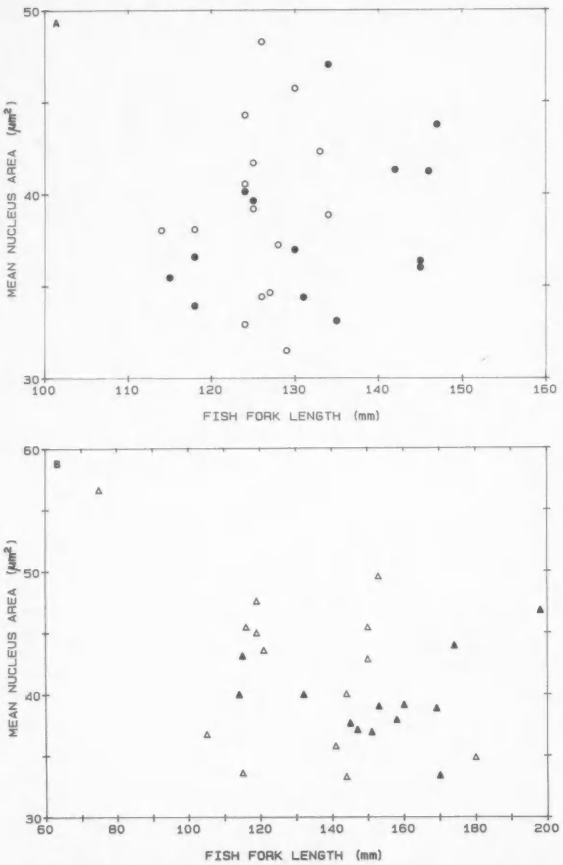

FIG. 4. Relationship between mean inter-renal nucleus area and fork length in (A) Atlantic salmon and (B) Arctic char. Solid circles indicate fish sampled from duoculture groups, open circles indicate fish from the monoculture groups.

was somewhat higher than in monoculture (1.152 versus 1.138), but the difference was not significant ($p = 0.089$).

When the two char strains were pooled, pooled char weight difference between treatments was significant on Day 135, the char weight in duoculture being on average 8.5% greater than in monoculture. The DC2 char were also significantly larger than the DC1 char (Mann–Whitney, $p<0.05$).

Fin Rot in Salmon

Incidence of dorsal fin rot had a clear tendency to be less in the duoculture salmon (Fig. 3). On Day 135, the difference between culture types was highly significant (Fisher–Irwin, $p<0.005$). No dorsal fin rot was observed in the char groups.

Blood Parameters and Inter-renal Histology

For salmon in monoculture, there were significant differences between replicates for all three parameters (Day 77, Table 6). Leucocrit values for the salmon replicates in duoculture were also significantly different. Char plasma chloride values were significantly different between replicates for both treatments, and significantly different for leucocrit between duoculture replicates.

There were no significant relationships in blood parameters between culture type, except for transformed leucocrit values in salmon. Culture type explains 27.6% of the variance of this parameter ($p<0.05$). There was no significant correlation between blood parameters and fin rot in individual Atlantic salmon.

There was no correlation between mean inter-renal cell nucleus area and blood parameters, or between mean area and fin rot in individual salmon.

Variation between mean nucleus area was significantly smaller for char in duoculture (F-test, $p = 0.024$), but there was no clear trend for salmon (Fig. 4).

Discussion

The growth of both Atlantic salmon and Arctic char of the Hammerfest strain was significantly better in duoculture, compared with monoculture. The analysis of variance showed a general effect of both culture treatment, species, and an interaction effect of these on fork length and weight which declined over time.

Salmon

Salmon in duoculture were superior in growth through the initial period of the experiment. Dorsal fin damage in aquaculture is mainly caused by aggression (nipping) (Abbott and Dill 1985). Atlantic salmon erect the dorsal fin in aggressive displays (Keenleyside and Yamamoto 1962), making the fin conspicuous and prone to being nipped. The less frequent occurrence of fin rot in salmon in duoculture could indicate decreased intraspecific aggression. Since Arctic char most often attack ventrally (Mork 1977), attack from the char would not affect the incidence of dorsal fin rot in salmon to the same degree. The same tendency is seen in the leukocrit values, these being higher in monoculture than duoculture. Social stress increase leucocrit level in rainbow trout (Peters et al. 1984), but the effect of stressors, in general, on leucocrit levels in salmonids are less clear (Wedemeyer and McLeay 1981).

The evenly dispersed salmon in duoculture could result in increased availability of feed to all individuals. Yamagishi (1962) showed for rainbow trout that differences in individual growth and mortality increased when food was restricted to a limited area. Holm and Fernö (1986) showed that parr of certain strains stayed near the bottom, and this could explain their observed frequent aggression as well as low utilization of food and a low growth rate.

Char

Arctic char may also have a lowered probability of delivering and receiving intraspecific acts of aggression in duoculture. Arctic char on average showed increased growth rate in duoculture, due to the increased growth rate in the Hammerfest individuals. The Skogseid strain was smaller than the Hammerfest strain. The growth rate was not clearly higher in duoculture, but the variation in growth rate was lower than in monoculture.

The differences in variance of mean inter-renal cell nucleus area in char suggest a weaker social hierarchy in duoculture. The overall mean for each culture type was, however, not different. This can be taken as an indication of a replacement of the monoculture type of stress (dominance hierarchy within the char population), with a stressor more evenly dispersed among

all individuals in the population. A stronger size-dependent hierarchy (Noakes 1980) in monoculture is also supported by the more homogenous growth rates among Skogseid char in duoculture.

If salmon aggression towards char is regulating char hierarchy, one must assume that: (1) the agonistic actions from salmon towards the Skogseid char are less size-specific than is intraspecific char aggression and/or (2) the salmon aggression has the same effect indirectly, by reducing aggression from larger towards smaller char. However, alternative (2) is contrary to the gain in growth among Hammerfest char in duoculture. Alternative (1) cannot be distinguished from a general breakdown of size-directed intraspecific aggression among the char.

The conclusion, therefore, is that the social hierarchy among char seems to have been changed by the presence of salmon. The increased growth rates in the Hammerfest groups in duoculture indicate that the gain achieved from reduced intraspecific aggression is greater than the costs per individual resulting from aggression from salmon. The performance difference in the two char strains is probably related to size and/or genetic differences.

Usefulness of the Physiological Parameters

Most of the physiological parameters differed little if at all between the culture types. Moreover, there was no correlation between fin rot and histological and blood parameters in individual fish. Holm (1989), dealing with more marginal duoculture effects, reached a similar conclusion; hematological and histological parameters do not provide additional insight. As an explanation, it should be emphasized that in intensive cultures, marginal differences in environmental conditions may cause clear differences in growth. There is a general tendency of inconsistency between parallels; this is also seen in the growth parameters. The masking effects of temperature on the hematological and histological parameters are obvious and well documented (e.g. Schreck 1981; Wedemeyer and McLeay 1981).

Therefore, it may be concluded that direct observation of fish behaviour combined with histology of the head kidney, observation of injuries resulting from aggression and individual growth measurements should provide a good basis for assessing the effects of duoculture on stress. Hematological measurements are easily carried out before fish dissection. They should be looked upon more as an indicator of other effects (e.g. diseases) than as a suitable parameter describing effects of social stress. The combination of direct observation of behaviour, histology, and injury resulting from aggression and growth are in accordance with Huntingford and Turner (1987), who emphasised that agonistic behaviour can be analyzed at least at three levels (behavioural, endocrinal, and neural), and that these interact in complex ways.

Duoculture in Aquaculture?

The observed positive growth effect illustrates the potential of duoculture. There were, however, indications (more distinct differences on Day 83 than 135) that the advantage of duoculture decreased throughout the experiment. According to Schreck (1981) and Pickering and Stewart (1984), a habituation among dominants and/or a compensation among subordinants can be postulated. If this is correct, the duoculture effect may be temporary. However, the size segregation may explain this decrease.

The mixing of species in duoculture could result in decreased intraspecific aggression by two means. First, when salmon disperse more evenly, the mean distance between conspecifics is increased. Second, the positioning of Arctic char among the salmon may reduce visual contact among salmon, partly through shading (Nortvedt and Holm 1988). The shading effect may be the main reason for dispersion of the fish, which thereby avoid aggression from conspecifics.

Ecological adaptations, in addition to the obvious size differences, can explain some of the differences in performance between the two char strains in duoculture. The Hammerfest strain shows an anadromous behaviour and is probably adapted to interact with more complex fish communities than the landlocked Skogseid strain, which originate from a lake with few other fish species. This may affect the behavioural adaptation of Hammerfest char, increasing their interspecific competitive success. Competition between Hammerfest char and salmon may also have been minimized through coevolution (Connell 1980). However, dominance based on size differences is important in behavioural interactions between salmonids (Gibson 1981).

Another trend of practical importance is the possible thermal effect. In period I with relatively high temperature, salmon grew at about the maximal growth rate, whereas Arctic char grew less than expected. In period II, temperature was low and the opposite growth pattern was observed; the char grew faster than the salmon. In a duoculture combination of Atlantic salmon and Arctic char, Mork (1977) found that char tended to be the most aggressive species in colder water (ca 10°C), while salmon were most aggressive in warmer water (ca 14°C). This indicates a relationship between aggressive activity and growth which can be regulated with temperature.

Duoculture of Atlantic salmon and Arctic char is possible on a commercial scale. Agonistic patterns for different candidate populations of both species should be judged carefully. Duoculture of Atlantic salmon and Arctic char is promising as a way to reduce intraspecific competition and enhance growth. However, even then competition may remain an important regulatory force. Competition may indicate that availability of food is insufficient, or it may be independent of food availability.

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Rapid Branchial Excretion of Dietary Quinoline by Rainbow Trout (*Salmo gairdneri*)[1]

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Excretion of the nitrogen heterocycle ^{14}C-quinoline was characterized in rainbow trout (*Salmo gairdneri*) following its ingestion with food. Quinoline-derived radioactivity was readily absorbed from the stomach as shown by peak serum levels that occurred 4–8 h after feeding. Pharmacokinetics were described using a two-compartment body model with first-order absorption and disposition; estimated half-lives for the α and β phase were 4.1 and 54.1 h, respectively. About 98% of the ingested dose was absorbed by gut epithelium before fecal excretion. Depending on dose, 71–83% of the ingested radioactivity was excreted during the first 24 h after feeding. Branchial elimination was the primary route of excretion since all other routes (fecal, biliary, urinary, and dermal) contributed <5% of the eliminated dose within 48 h after ingestion. There was evidence for saturation of minor excretory pathways as the dose was increased from 1 to 100 mg quinoline·kg^{-1} body weight. Apparent spillover occurred into the branchial route at the 100 mg·kg^{-1} dose. Dietary quinoline was eliminated across the gills as parent compound, independent of the dose.

L'excrétion de la quinoléine-^{14}C hétérocyclique a été déterminée dans la truite arc-en-ciel (*Salmo gairdneri*) après avoir été ingérée avec de la nourriture. La radioactivité dérivée de la quinoléine a été facilement absorbée de l'estomac, comme le montrent les niveaux maximum dans le sérum qui se sont produits entre 4–8 h après l'ingestion. La pharmacocinétique a été décrite à l'aide d'un modèle à deux compartiments comportant l'élimination et l'absorption de premier ordre; les demi-vies estimées pour les phases α et β ont été respectivement de 4,1 et 54,1 h. Environ 98 % de la dose ingérée a été absorbée par l'épithélium de l'intestin avant excrétion fécale. Selon la dose, 71–83 % de la radioactivité ingérée ont été éliminés au cours du premier 24 h après l'ingestion. L'élimination par les branchies a été la principale voie d'excrétion puisque toutes les autres voies (fécale, biliaire, urinaire, dermique) ont contribué moins de 5 % de la dose éliminée 48 h après l'ingestion. La saturation des trajectoires d'excrétion secondaire a été montrée lorsque la dose a été augmentée de 1 à 100 mg de quinoléine·kg^{-1} de poids corporel. Une certaine quantité de quinoléine a semblé passer par la voie branchiale à la dose de 100 mg·kg^{-1}. La quinoléine absorbée dans le régime alimentaire a été éliminée par les branchies sous forme de composé parental, peu importe la dose.

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The fate of nitrogen-heterocyclic compounds in the aquatic environment has been of recent concern because of links to hepatic lesions in bottom fish (Roubal and Malins 1985). That nitrogen-containing aromatic compounds persist in the aquatic environment is evident by their presence in sediments from polluted estuaries (Krone et al. 1986). These studies and others indicate that chemicals within this general compound class are bioavailable to fish and fish food organisms.

Quinoline is a two-ring nitrogen-heterocyclic compound that occurs in many industrial products, petroleum, shale oil, and coal liquefaction materials (Weisburger and Williams 1980; Wright and Later 1985). Thus, it may enter aquatic ecosystems from waste effluents, surface water spills or it could be leached from energy-derived waste materials into the groundwater (Zachara et al. 1986). Quinoline is important from an environmental risk perspective because it is rapidly absorbed from the water by fish and aquatic invertebrates (Southworth et al. 1980; Bean et al. 1985; Dauble et al. 1985). In addition, it is a known hepatocarcinogen in mice and rats (Hirao et al. 1976; Shinohara et al. 1977) and is mutagenic in Ames assays (Nagao et al. 1977; Hollstein et al. 1978).

Most studies of the fate of organic contaminants in fish have focused on tissue distribution and metabolism of stored residuals because of the potential links to human health. Little attention has been focused on the specific mechanisms of excretion for xenobiotics potentially ingested by fish. A previous study showed that rainbow trout (*Salmo gairdneri*) rapidly eliminated quinoline following dietary exposures (Dauble et al. 1987).

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However, the physiological mechanisms involved in excretion, including the role of biotransformation, were unknown.

The objective of our study was to determine the relative importance of major excretory pathways in the elimination of dietary quinoline by juvenile rainbow trout and to characterize mechanisms of excretion following ingestion. Pharmacokinetics, absorption, and rates of gastrointestinal movement of ^{14}C-quinoline were determined following ingestion at potential environmental concentrations, and the chemical form of excreted radioactivity was characterized. The effect of dose on mechanisms of elimination was also examined.

Methods

Animals

Juvenile rainbow trout, Kamloops strain, were used for all experiments. Fish obtained from stocks reared at Pacific Northwest Laboratory (PNL) were placed in individual 20-L glass aquaria for 7–10 d before testing to facilitate voluntary feeding. Handling during experimentation was minimized to reduce interactions of stress with mechanisms of excretion. Exposure temperatures were maintained at 12°C by a water bath for all studies and fish were held on a 12-h light:dark cycle.

Chemicals

Uniformly-labelled ^{14}C-quinoline (8.83 mCi/mM) was synthesized by Pathfinder Labs, Inc. (St. Louis, MO) and purified (>99%) at PNL by liquid chromatography before use. Quinoline, 5-hydroxyquinoline, 4-hydroxyquinoline, and 8-hydroxyquinoline glucuronide standards were obtained from Aldrich. The NCS tissue solubilizer and PCS scintillation mixture were purchased from Amersham/Searle. All solvents were Burdic and Jackson "distilled in glass" grade.

Diet and Feeding

Food pellets were prepared for each test according to methods described in Dauble et al. (1987). Individual doses were calculated by liquid scintillation counting of a subsample to obtain milligram-equivalent quinoline and then dividing food weight by postexposure fish weight. All feeding was at 1% body weight·d^{-1}. Fish that did not consume their total daily ration within 10 min of feeding were not used in the analysis; most ate all food within 15 s.

Excretory Route Studies

Juvenile trout (24–49 g) were individually isolated in separate aquaria, starved for 48 h, then fed a single dose of radiolabelled quinoline (1.6 mg·kg^{-1} dose) in a reformed food pellet. At 1, 2, 4, 8, 16, 24, 36, and 48 h after feeding, fish (N = 3–5) were removed and immobilized in an ice bath. Urine samples were taken by pressing the bladder and collecting urine in calibrated glass capillary tubes. Blood was collected by severing the caudal peduncle; duplicate 100-mL serum samples were obtained after centrifugation at 2000 g for 10 min. Epidermal mucus was scraped from the dorsal portion of the lateral line and placed in preweighed glass scintillation vials. The liver, gallbladder plus bile, anterior and posterior kidney, and gill filaments were dissected, rinsed in distilled water, blotted, and placed in preweighed vials for liquid scintillation counting. Digestive tract contents were taken from the stomach, pyloric caeca, upper intestine, mid-intestine, and rectum. Concentrations of radioactivity in the food and digestive tract were equalized based on dry weight determinations (APHA 1980) of gut contents from other fish. Tissue samples were analyzed for total radioactivity as described in Dauble et al. (1987). Aquaria water was continuously recirculated through an air-life carbon filter during the static exposures. Duplicate 1-mL water samples were taken at each tissue sampling interval to monitor for residual radioactivity.

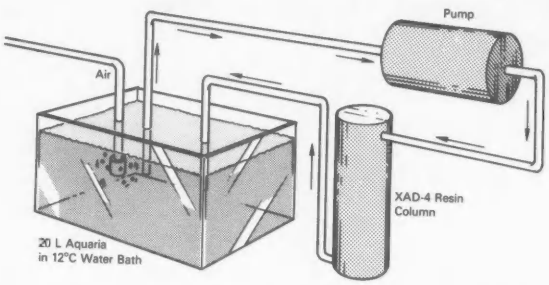

FIG. 1. Flow-through system used to collect excreted radioactivity from rainbow trout.

Additional experiments were conducted to clarify the importance of urinary excretion. Repeated measurements of total radioactivity in trout urine were made from individual fish (N = 4) at 4-h intervals for 24 h following feeding. Total excretion of the ingested dose was estimated based on mean measured urine concentrations and estimates of urine flow reported for freshwater-adapted rainbow trout (Hickman and Trump 1969; Hunn 1982).

Injection Studies

Fish (45–72 g) were injected intraperitoneally with ^{14}C-quinoline to monitor flux across the gills independent of potential contamination from oral dosing. Each fish received a 0.8-mg·kg^{-1} dose in 0.1-mL saline; water and gill concentrations were determined as described before at 0, 4, 8, and 24 h post-injection. Tissue and water measurements (N = 2) were taken from paired exposures: aerated only and with recirculating carbon filters.

Dose-Disposition Studies

Fish (18–28 g) were separated into three treatment groups for feeding: 1 mg·kg^{-1}, 10 mg·kg^{-1}, and 100 mg·kg^{-1} doses. Whole-body elimination to aerated aquaria was measured for one group of fish (N = 3). Rates of excretion were estimated based on water concentrations at 0, 1, 2, 4, 6, 8, 12, 16, and 24 h postfeeding. Total radioactivity for separate 1-mL samples was measured by liquid scintillation counting.

Relative body burden at 24-h postfeeding was determined for a separate group of fish that were maintained in carbon-filtered aquaria (N = 5). Samples taken included contents of stomach and intestine, liver, gallbladder plus bile, kidney, muscle, brain, mesenteric fat, and carcass (remaining tissue). Muscle and carcass samples were homogenized and subsampled to determine total radioactivity.

Metabolism Studies

Fish (20–28 g) were isolated and fed a single dose of quinoline at 1 mg·kg^{-1}, 10 mg·kg^{-1}, and 100 mg·kg^{-1} (N = 2),

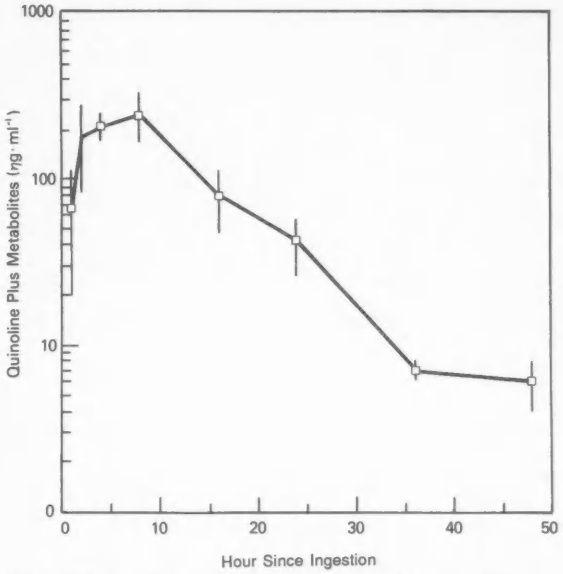

FIG. 2. Pharmacokinetics of quinoline plus metabolites in the serum of rainbow trout following a single feeding at 1.6 mg quinoline·kg^{-1} body weight. Values shown are mean ± SE, N = 4–5.

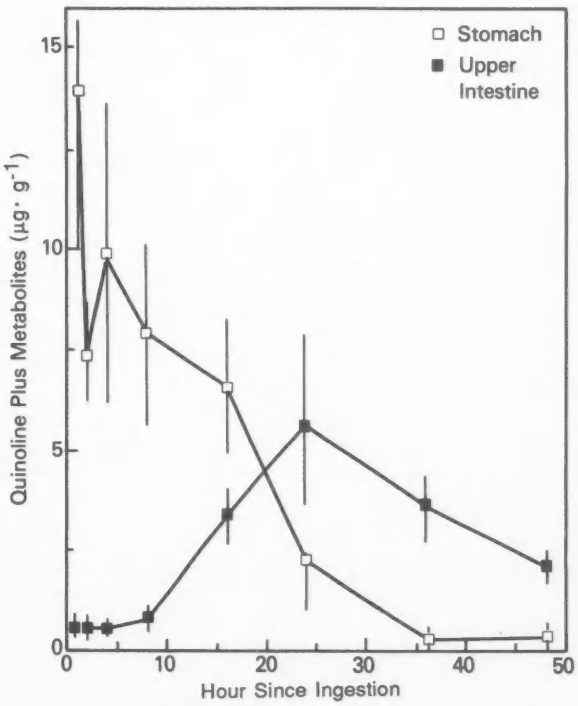

FIG. 3. Concentration of quinoline plus metabolites in the stomach and intestine of the rainbow trout during passage of the food bolus. Trout were fed once at 1.6 mg quinoline·kg^{-1} body weight. Values shown are mean ± SE, N = 4–5.

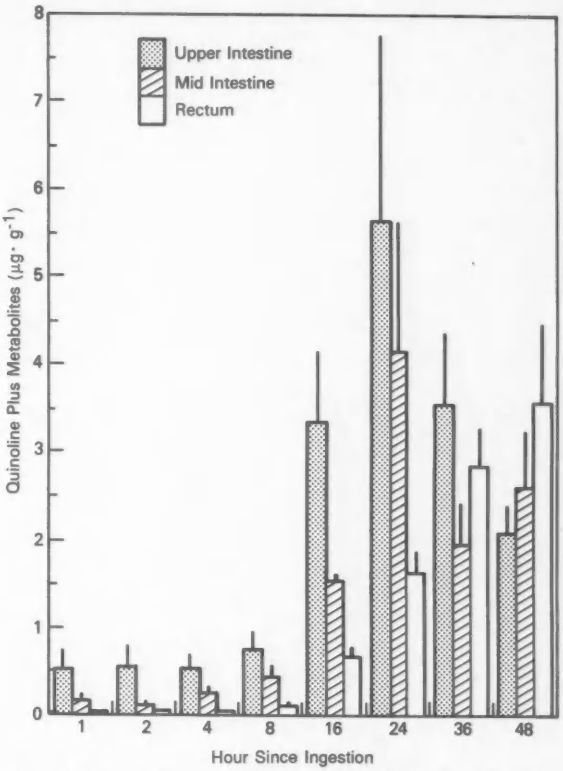

FIG. 4. Changes in mean concentration of quinoline-derived radioactivity during movement of the food bolus through the lower digestive tract of rainbow trout. Vertical bars are 1 SE, N = 4–5.

maintained in aquaria water from 0–8 h after feeding, then removed. A recirculating chemical extraction system (Fig. 1) was set up immediately after feeding to determine the chemical form of excreted radioactivity. Water was pumped through a precleaned XAD-4 resin column (Junk et al. 1974) at 25 mL·min^{-1}. Water samples were periodically collected from the aquaria water and after column passage to determine trapping efficiency. Aquaria water was filtered for 12 h after feeding. The resin column was stored overnight at 4°C before extraction with three successive 10-mL washes of distilled ether. The water:ether ratio eluted from the column was adjusted to 1:3 and made acidic (pH 2) by addition of 1 N H_2SO_4. The solution was shaken vigorously for 5 min in a 50-mL glass-stoppered vial, and 100-mL aliquots were removed from both aqueous and ether fractions to determine extraction efficiency.

A 2-mL subsample from the aqueous fraction was neutralized with 0.5 N NaOH, sparged with N_2 at 10 lb·in^{-2} for 5 min, then analyzed for parent compound and metabolites using reverse-phase high pressure liquid chromatography (HPLC). Analysis by HPLC was conducted using a solvent delivery system of 60:40, methanol:water at 1 mL·min^{-1} and a Beckman 5-μM ultrasphere C8, 25-cm × 4.6-mm column. Concentration of parent compound was determined by calculating relative peak area at 254-μM absorbance for duplicate 15–50 mL injections. Fractions were collected at 30-s intervals, and recovered radioactivity compared with retention time of known standards.

TABLE 1. Concentration of quinoline plus metabolites $ng \cdot g^{-1}$) in excretory tissues and serum of rainbow trout following ingestion of ^{14}C-quinoline at 1.6 $mg \cdot kg^{-1}$ dose. Values as mean ± SD, $N = 3$.

Tissue	Time since ingestion (h)							
	1	2	4	8	16	24	36	48
Gill	847 ± 369	673 ± 233	545 ± 93	431 ± 133	135 ± 5	24 ± 7	8 ± 1	14 ± 7
Liver	324 ± 114	410 ± 93	420 ± 161	331 ± 102	204 ± 40	79 ± 18	35 ± 4	33 ± 10
Gallbladder plus bile	227 ± 96	466 ± 57	561 ± 206	929 ± 332	5129 ± 1054	4574 ± 456	5236 ± 179	5165 ± 1212
Anterior kidney	442 ± 158	496 ± 116	338 ± 80	244 ± 50	58 ± 9	53 ± 8	24 ± 5	29 ± 10
Posterior kidney	207 ± 84	93 ± 17	154 ± 33	136 ± 26	176 ± 59	96 ± 12	45 ± 11	65 ± 19
Serum	68 ± 48	189 ± 102	210 ± 46	248 ± 90	80 ± 37	42 ± 16	7 ± 1	6 ± 2

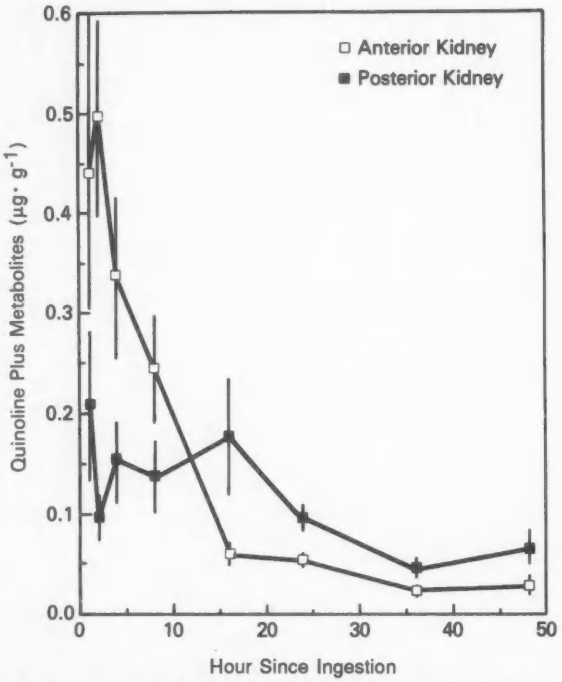

FIG. 5. Patterns of quinoline-derived radioactivity in the anterior (K_1) and posterior (K_2) section of the trout kidney following ingestion of ^{14}C-quinoline values are mean ± SE, N = 4–5.

Statistical Analysis

Kinetic parameters were determined using a two-compartment body model with first-order absorption and disposition; serum clearance data were resolved into distribution (α) and elimination (β) phases by curve stripping (O'Flaherty 1981). Significance testing was conducted using analysis of variance (ANOVA) and the *t*-test for paired comparisons (Sokal and Rohlf 1981). Estimates of whole-body elimination rates were based on the mean percent of the administered dose excreted to the water.

Results

Absorption, Transport, and Clearance

Quinoline-derived radioactivity was readily absorbed by rainbow trout after dietary exposure; maximum serum concentrations occurred from 2 to 8 h after ingestion (Fig. 2). Levels of radioactivity declined rapidly after they peaked, and mean serum concentrations at 36 h were <2% of those at 8 h. The elimination portion of the curve (8–48 h postingestion) was characterized by a distribution (α) phase with an estimated serum half-life of 4.1 h and an elimination (β) phase with a half-life of 54.1 h

Only 8.0–12.7% of the ingested dose was recovered in the digestive tract 2 h after feeding ($N = 2$). We found that 3.5–9.0% and 1.1–2.2% of the ingested dose remained at 16 and 24 h, respectively. Based on differences observed between maximum concentrations observed in the stomach and those in the intestine of individual fish, 56–74% of the quinoline was absorbed from the stomach. About 87% of the total ingested dose was absorbed by the time the food bolus reached the mid-intestine at 24 h.

Quinoline associated with the food was transported from the stomach to the upper intestine at 8–16 h following ingestion (Fig. 3). Less than 8% of the ingested dose remained in the stomach at 8 h. Maximum concentrations of quinoline plus metabolites were measured at 24 h in the upper region of the intestine. Quinoline-derived radioactivity in the rectum was highest at 48 h after ingestion (Fig. 4). Equalized concentrations of radioactivity were determined as anterior intestine > mid-intestine = rectum.

Temporal patterns of quinoline plus metabolites present in excretory tissues are summarized in Table 1. Rapid disposition of radioactivity to the gills, liver, and kidney was evident. Maximum concentrations were observed in the gill at 1 h, and levels remained higher than liver and kidney tissue for the first 8 h following ingestion. Uptake patterns for the liver were similar to those observed in the serum. Although there was high variation for the anterior and posterior kidney samples, significant differences were found between the two regions in patterns of stored quinoline residues (ANOVA, $p = 0.001$). Mean maximum concentrations of radioactivity in the posterior kidney were only 42% of those detected in the anterior kidney (Fig. 5).

Characterization of Excretory Routes

Maximum concentrations of quinoline and metabolites were found in the urine at 4–16 h after ingestion; mean concentrations declined to 15% of peak values by 48 h. Mean urine-to-serum ratios (U/S) were near unity for the first 8 h following ingestion. However, mean U/S values increased to 6.3 at 16 h and 24 h, 9.8 at 36 h, and 20.5 at 48 h. Urinary excretion

TABLE 2. Urinary excretion of quinoline plus metabolites following ingestion and intraperitoneal injection of ^{14}C-quinoline. For treatment of fish see methods. Dose excreted based on 75 mL·h^{-1}·kg^{-1} fish urine flow rate and measurements of mean urine concentrations (N = 3–5).

Method[a]	Feeding dose (mg·kg^{-1})	Peak excretion		Percent of dose excreted	
		Interval (h)	Concentration (mg·mL^{-1})	0–24 h	24–48 h
Independent	1.6	8–16	0.56	1.6	0.5
Repeated	1.0	4–8	0.17	0.8	no data

[a]Separate fish were each measured once to obtain independent measurements and fish were measured two or three times over a 24-h period for repeated measurements.

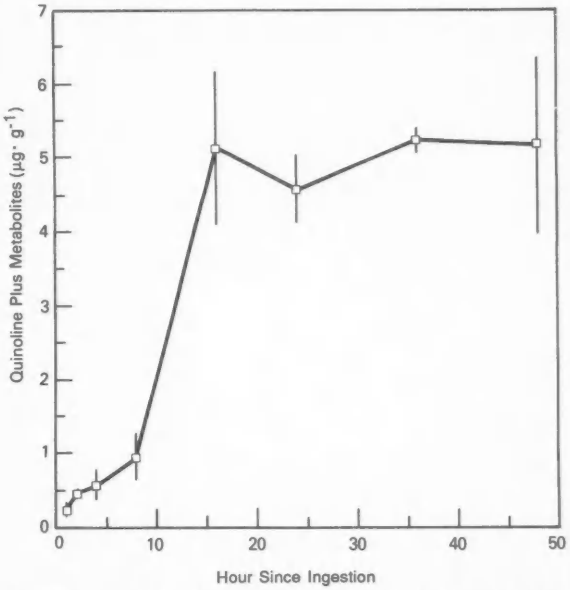

FIG. 6. Accumulation of quinoline plus metabolites in the gallbladder bile of rainbow trout following ingestion of a single meal containing ^{14}C-quinoline. Values are mean ± SE, N = 4–6.

TABLE 3. Changes in gill/serum concentrations or apparent flux of quinoline across trout gills following injection at 0.8 mg·kg^{-1} dose. Water and tissue concentrations are the average from two fish.

Sample treatment	Interval (h)	Concentration (ng·mL^{-1} or ng·g^{-1})		
		Water	Gill	Serum
Filtered aquaria	4	0.22	8.24	14.24
	8	0.17	5.06	8.85
	24	0.05	1.13	2.20
Nonfiltered aquaria	4	1.32	9.50	15.23
	8	1.42	9.26	16.45
	24	1.52	16.48	8.10

accounted for an estimated 1.6% of the ingested dose for the first 24 h following ingestion, when independent measurements from separate fish were used (Table 2). The lower values estimated for urinary excretion (0.8%), taken during repeated measurements (handled fish), may be attributable to increased urine output following acute hypoxic stress (Hunn 1982).

Bile volume decreased for the first 8 h following feeding, then increased at 48 h to about 73% of preexperimental volume. Amounts of quinoline-derived radioactivity present in the gallbladder generally paralleled these trends (Fig. 6). Mean values for total radioactivity found in the gallbladder and bile of rainbow trout ranged from 0.02% of the dose at 4 h postingestion to 1.1% of the dose at 48 h. Maximum observed values represented 1.9% of the ingested dose.

Total radioactivity present in the lower digestive tract (pyloric caeca to rectum) ranged from 0.13% of the ingested dose at 1 h postfeeding to 5.28% of the dose at 16 h postfeeding. Maximum amounts measured in the rectum did not exceed 2.2% of the dose. Mean values obtained for individuals sampled from 24–48 h (N = 6) were <0.8% of the ingested dose and represented the portion available for fecal excretion.

There was no evidence for secretion of quinoline or its metabolites in skin mucus. Levels of radioactivity from mucus did not exceed residual levels measured in aquaria water.

Although branchial excretion was not measured, indirect evidence (i.e. measurement of all other potential pathways) indicated that this route accounted for about 95% of the total excretion of quinoline-derived radioactivity by rainbow trout. The injection experiments, designed to measure flux of radioactivity across the gills, demonstrated that movement of quinoline occurred readily from the blood across gill epithelium. A nearly constant concentration gradient was maintained between concentrations of radioactivity in the serum and the gill at water concentrations from 0.05 to 1.64 ng·mL^{-1}, following intraperitoneal injection (Table 3). Gill and serum concentrations decreased rapidly as quinoline was removed from the water by filtration, but remained high for fish held in unfiltered aquaria. Further evidence for a high rate of gill flux was shown where gill:water concentration ratios of fish held in carbon-filtered aquaria (low residual radioactivity) were nearly four times greater than ratios from fish allowed to depurate into nonfiltered aquaria.

Effects of Dose on Disposition and Clearance

In general, concentrations of quinoline and metabolites stored in tissues increased in direct proportion to the dose administered in food (see concentration ratios, Table 4). However, differences in this trend were observed for some tissues at the higher doses. For example, concentrations in the gills were about 1.6 and 2.7 times those predicted for a linear response at the 10-mg·kg^{-1} and 100-mg·kg^{-1} doses, respectively. At the 100-mg·L^{-1} dose, the gallbladder bile had concentrations about 34% of those predicted.

Tissue:serum ratios were near unity for all but the most highly perfused tissues (i.e. liver, kidney, gills) and the gallbladder bile (Table 4). These ratios were independent of dose for most tissues. However, quinoline appeared to have a greater affinity

TABLE 4. Tissue concentrations at 24 h postingestion for three oral doses. Values shown as mean ± SE, $N = 5$. Concentration ratios are based on concentrations relative to those measured following the 1 mg·kg^{-1} dose.

Tissue	Dose (mg·kg^{-1})	Concentration (ng·g^{-1})	Concentration ratio	Tissue/Serum
Serum	1	5 ± 1	1	1.0
	10	69 ± 12	14	1.0
	100	370 ± 220	74	1.0
Brain	1	7 ± 2	1	1.4
	10	66 ± 11	9	1.0
	100	630 ± 350	90	1.7
Fat	1	10 ± 4	1	2.0
	10	100 ± 20	10	1.4
	100	1150 ± 630	115	3.1
Liver	1	25 ± 6	1	5.0
	10	287 ± 39	11	4.2
	100	1870 ± 910	75	5.1
Gallbladder plus bile	1	2103 ± 450	1	420.6
	10	23213 ± 3664	11	336.4
	100	78470 ± 35600	34	212.1
Gill	1	13 ± 4	1	2.6
	10	207 ± 120	16	3.0
	100	3490 ± 2580	268	7.2
Kidney	1	52 ± 9	1	10.2
	10	576 ± 51	11	8.3
	100	3130 ± 1720	60	8.5
Muscle	1	3 ± 1	1	0.6
	10	40 ± 6	13	0.6
	100	170 ± 90	57	0.5
Carcass	1	7 ± 2	1	1.4
	10	78 ± 7	11	1.1
	100	750 ± 450	107	2.0

TABLE 5. Distribution of quinoline plus metabolites in tissues of rainbow trout. Values as percent body burden retained, 24 h after a single feeding (mean ± SD, $N = 5$).

Tissue	Ingested doses		
	1 mg·kg^{-1}	10 mg·kg^{-1}	100 mg·kg^{-1}
Kidney	0.4 ± 0.1	0.3 ± 0.1	0.3 ± 0.1
Gill	0.3 ± 0.3	0.5 ± 0.8	1.0 ± 1.3
Liver	0.4 ± 0.2	0.2 ± 0.1	0.8 ± 0.9
Gallbladder	80.9 ± 5.1	80.3 ± 8.2	73.8 ± 14.0
Fat	<0.1	<0.1	<0.1
Brain	0.3 ± 0.1	0.3 ± 0.2	0.4 ± 0.2
Muscle	0.9 ± 0.1	1.0 ± 0.2	0.9 ± 0.4
Carcass	5.9 ± 1.1	6.5 ± 3.1	10.3 ± 7.5
Stomach contents	2.6 ± 4.6	1.3 ± 2.3	1.7 ± 3.9
Intestinal contents	8.4 ± 1.8	9.6 ± 5.8	11.1 ± 9.1
Percent of ingested dose stored	11.0 ± 4.7	12.3 ± 3.9	5.4 ± 5.9

for gill tissue at the 100-mg·kg^{-1} dose versus the two lower doses.

Distribution of quinoline-derived radioactivity was not significantly different at the range of doses tested (Table 5). About 80% of the body burden remaining at 24 h postfeeding was contained in the gallbladder bile, and an average of 11% of the dose remained unabsorbed in the digestive tract. Relative body burden for remaining tissues was carcass> muscle> gills≥ liver≥ kidney= brain> fat (Table 5). The percentage of the total ingested dose retained by fish fed 100 mg quinoline·kg^{-1} was about half that for fish fed the two lower doses.

TABLE 6. Cumulative rate of total excretion (as percent of the dose) for quinoline following ingestion at 1, 10, 100 mg·kg^{-1} dose. Values are based on the amount of radioactivity present in aquarium water (mean ± SD, $N = 3$).

Hour since feeding	Percent excretion at ingested dose		
	1 mg·kg^{-1}	10 mg·kg^{-1}	100 mg·kg^{-1}
1	4 ± 1	4 ± 2	7 ± 2
2	9 ± 2	5 ± 1	35 ± 18
4	19 ± 3	14 ± 2	63 ± 27
6	35 ± 2	28 ± 3	63 ± 24
8	53 ± 6	55 ± 15	65 ± 18
12	68 ± 2	58 ± 1	73 ± 14
16	63 ± 7	73 ± 3	80 ± 11
24	71 ± 2	75 ± 3	83 ± 3

Whole-body elimination, based on percent of total dose excreted, was similar for the 1- and 10-mg·kg^{-1} doses at all intervals from 0–24 h postingestion. Rates of excretion were greatest during the first 8 h after ingestion when >50% of the dose was eliminated (Table 6). However, the rate of excretion for the 100-mg·kg^{-1} dose was nearly twice that of the two lower doses for 0–6 h postingestion. Variability of organism response appeared to be related to dose; coefficient of variation was highest for the 100-mg·kg^{-1} dose. Total excretion at 24 h postingestion was similar for each treatment and ranged from 71–83% of the ingested dose.

Chemical Form of Excreted Radioactivity

Trout excreted 53–65% of the ingested dose during the 8-h metabolism studies. We extracted about 18 L of water during

TABLE 7. Relative contribution of minor excretory pathways following ingestion of ^{14}C-quinoline by rainbow trout. Values represent the mean percent of fed dose accounted for to 48-h postingestion (total excretion was >70% of the fed dose at 24 h).

Excretory pathway	Percent of dose excreted
Biliary	1.1
Fecal	0.8
Urinary	2.1
Dermal	<0.1

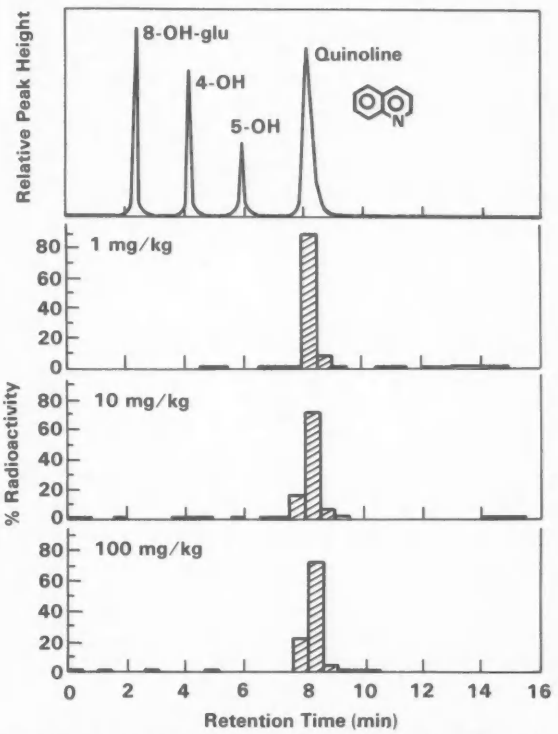

FIG. 7. Representative HPLC chromatogram of quinoline and metabolite standards and profiles of radioactivity excreted into the water at three oral doses. HPLC fractions were collected at 30-s intervals and recovered radioactivity was calculated based on total radioactivity injected into the column.

the 12-h extraction interval to obtain an average of 17% of the individual ingested dose from the aquaria water. Overall extraction efficiency of radioactivity from the water on the XAD column was >95%. Recovery of radioactivity from the XAD column using the ether extraction method was >96%. An average of 95% of the radioactivity remained in the aqueous fraction that was subsequently analyzed for parent compound and metabolites.

Retention time for quinoline ranged from 7.86 to 8.18 min for the six fish (N = 2 each treatment). Overall recovery of radioactivity during HPLC analysis was >99%. The percent of radioactivity associated with the quinoline peak ranged from 94.3 to 97.8% of the injected radioactivity. This indicated that almost all quinoline was excreted as parent compound. No peaks representing individual metabolites were detected for any of the three feeding doses (Fig. 7). The sample fraction containing compounds more polar than quinoline ranged from only 0.8–1.7% of the total recovered radioactivity.

Discussion

Peak serum concentrations of quinoline-derived radioactivity in serum occurred before most of the ingested dose reached the alkaline environment of the intestine. This indicated that quinoline is readily absorbed in the stomach of rainbow trout when not highly bound in a food matrix. Different kinetics for gastrointestinal uptake may occur for quinoline bound to sediment or to food organisms. However, our studies represent basic disposition of ingested quinoline by rainbow trout. Studies with mammals have shown drug uptake across absorptive epithelia is governed mainly by physical processes and can be predicted from the dissociation constant and lipid-solubility of the undissociated drug moiety (Hogben et al. 1957, 1959). The gastric mucosa of both humans and rats is known to be selectively permeable to the undissociated form of drugs (Schanker et al. 1957; Hogben et al. 1957). That quinoline (pKa = 4.9) was absorbed in the stomach is evidence that it existed in the unionized form and diffused through the stomach epithelium into the blood. Gastric emptying time was likely delayed because of the single feeding, and this probably also influenced the absorption rate of quinoline. Passage time of a drug in a particular segment of the digestive system, rather than the absorptive capacity of that segment, is thought to be the crucial factor in determining the amount of compound absorbed (Levine 1970).

We found that trout efficiently absorbed quinoline from the digestive tract. Almost all of the total ingested dose was absorbed by gut epithelium and therefore not available for fecal excretion. A significant contribution of biliary excretion to fecal excretion was unlikely given time courses for gallbladder accumulation of radioactivity and bile retention (see Fig. 6). Additionally, measurements of radioactivity in the digestive tract over time support the hypothesis that the unabsorbed dose was quite low. Thus, lack of significant bioaccumulation of dietary quinoline by rainbow trout (Dauble et al. 1987) is related to rapid excretion, rather than to inefficient absorption.

Branchial excretion was implicated as the primary route of excretion because all other possible routes of elimination contributed to <5% of the total eliminated dose during the first 48 h after ingestion (Table 7). Rapid excretion of a xenobiotic by fish can occur across the gills because this organ has a high surface area, receives the entire cardiac output, and is ventilated by large volumes of water. Other teleost excretory routes (i.e. renal, biliary) are more limited in their ability to rapidly excrete xenobiotics because they are dependent upon active processes. That absorbed quinoline was efficiently eliminated as parent compound across the gills is consistent with its physical and chemical characteristics (molecular weight, 129; log octanol:water partition coefficient, 2.03). McKim et al. (1985) found that chemicals with log octanol:water coefficients <3 were rapidly eliminated across the gills. Branchial excretion of quinoline is also in accordance with studies conducted by Hunn and Allen (1974a) using quinaldine (3-methylquinoline).

Lipid solubility is another factor important for branchial excretion of chemicals. For example, Maren et al. (1968) reported that the more highly lipid-soluble drugs were excreted more rapidly across the gills of doggfish (*Squalus acanthus*) than the more polar compounds. In contrast, Thomas and Rice (1982) found that the size of aromatic hydrocarbons was a more important factor than partition coefficient in branchial excretion

of xenobiotics fed to Dolly Varden char (*Salvelinus malma*). However, passive diffusion can occur across any barrier that is permeable to the chemical and across which a concentration gradient exists. This process appears to be the principle mechanism for elimination of dietary quinoline.

At higher doses, the minor excretory pathways (i.e. renal, biliary) may have become saturated. Evidence that saturation occurred was suggested by the decreased concentrations of radioactivity in kidney and bile, relative to dose, as the dose was increased from 1 to 100 $mg \cdot kg^{-1}$. Concomitant increases in gill concentrations and the gill:serum ratio occurred at the higher doses, indicating that as rates of urinary and biliary excretion were saturated, a spillover occurred into the branchial route.

Because quinoline is eliminated as parent compound, biotransformation only plays a minor role in excretion. Although metabolism may not be quantitatively important for compounds that rapidly diffuse through gill membranes, it influences both the form and persistence of stored quinoline derivatives. The role of metabolism in urinary excretion was suggested by temporal changes in the U/S ratio. Our observation of increased U/S ratios with time may indicate the presence of water-soluble metabolites, forms less likely to be passively absorbed and more likely to be secreted by renal tubules (Pritchard and James 1982). The slow rate of excretion of quinoline and metabolites via urine is similar to results obtained by Hunn and Allen (1974b) following exposure of channel catfish (*Ictalurus punctatus*) to quinaldine. A heterogenous pattern of radioactivity in the kidney of rainbow trout (see Table 1) was also reported by Gingerich (1986) following intravenous injection of the piscicide rotenone and by Balk et al. (1984) who exposed northern pike (*Esox lucius*) to (^{3}H)benzo(*a*)pyrene in food. Although the trout kidney does not appear morphologically distinct, there are differences: the head portion consists of lymphoid, hematopoietic, interrenal, and chromaffin tissue, while modification and storage of urine occurs in the posterior end of the kidney and in the urinary bladder (Hickman and Trump 1969). Thus, storage and elimination of xenobiotics in the renal system of fish may be related to differences in both the structure and the functional role of kidney tissues.

That hepatic metabolism of quinoline is relatively slow was indicated by the appearance of relatively low concentrations of radioactivity in the bile until nearly 16 h after ingestion. This indicates that quinoline may have a low hepatic extraction rate in rainbow trout, i.e. first-pass metabolism is insignificant. Biliary excretion would not be expected to be a major route of excretion for quinoline because of its molecular weight, polarity, or structural factors (Smith 1973). Biliary excretion is a major route of excretion (50%) for benzo(*f*)quinoline in rats (Birnbaum and Johnson 1985); benzo(*f*)quinoline is also extensively metabolized before urinary excretion. However, comparisons of excretion per se are difficult because ventilatory routes are often different among animal groups. Previous studies have shown that metabolism is a prerequisite for elimination of quinoline via the bile by rainbow trout (Bean et al. 1985; Dauble et al. 1987). Although not quantitatively important in excretion, metabolism of quinoline by hepatic tissue can lead to more biologically active forms (LaVoie et al. 1983), including free radicals associated with hepatic neoplasms (Roubal and Malins 1985).

Dietary contaminants that are excreted slowly are likely to be more important because of their persistence and increased potential for binding to cellular constituents. Because quinoline-derived radioactivity is retained in tissues mainly as biotransformation products (Bean et al. 1985; Dauble et al. 1987), biological activity would likely be limited to metabolites. This concept is consistent with the hypothesis posed by LaVoie et al. (1983) that the formation of 5-6-epoxy-5-6 dihydroquinoline is associated with the activation of quinoline to a mutagen/carcinogen in other organisms.

Bioaccumulation potential for chemicals taken up by fish in their diet depends both on the efficiency of uptake and the clearance rate of the compound. Although biotransformation processes may be rapid enough to detoxify some compounds (Lech and Statham 1975), other absorbed compounds (like quinoline) may have characteristics that allow elimination by passive diffusion across the gills.

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Imprinting and Homing of Atlantic Salmon (*Salmo salar*) Kelts

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Experiments were conducted to determine if a process similar to imprinting occurs during each seaward migration of Atlantic Salmon (*Salmo salar*). Displaced Atlantic salmon kelts homed to the site from which they had previously emigrated to sea as smolts (Big Salmon River, New Brunswick, Canada) and did not home to their release sites, or their overwintering sites 150 km away. Delaying release of kelts past the time of normal seaward migration did not cause the behavioral changes associated with interference of the imprinting process described for smolts. Delayed release kelts did not remain near their seawater or estuarine release sites, home to their release sites, or non-selectively home to suitable spawning streams near their release sites. Delayed released kelts travelled away from the release site faster than kelts released during their normal time of seaward migration, but they did not return either to Passamaquoddy Bay or their natal stream in the calendar year of their release (the normal time for this stock) or in subsequent years.

Des expériences ont été réalisées afin de déterminer si un phénomène s'apparentant à l'imprégnation se produit au cours de chacune des migrations vers la mer du saumon de l'Atlantique (*Salmo salar*). Des saumons vides de l'Atlantique, déplacés, sont remontés au lieu d'où, smolts, ils avaient émigré en mer (rivière Big Salmon, Nouveau-Brunswick) au lieu de retourner aux lieux de lâcher des saumons vides (après le moment normal de la migration vers la mer) n'a pas entraîné les modifications comportementales qui sont généralement associées à des perturbations du phénomène d'imprégnation décrit pour les smolts. Ainsi, les saumons vides dont le lâcher a été retardé ne sont pas restés près des lieux de lâcher estuariens ou marins, n'y sont pas retournés et n'ont pas non plus cherché des cours d'eau qui leur conviendraient pour frayer. Ces saumons vides se sont éloignés des sites de lâcher plus vite que les saumons vides relâchés durant la période normale de migration vers la mer, mais ne sont ni retournés à la baie Passamaquoddy, ni à leur rivière natale au cours de l'année du lâcher (c'est-à-dire la période normale pour ce stock), ni dans les années subséquentes.

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The olfactory imprinting hypothesis explaining salmon homing states that at smoltification juvenile salmon imprint to the unique odors of their natal stream and subsequently use these cues to locate the same stream during their spawning migrations (Hasler and Scholz 1983). There are three basic types of evidence supporting the olfactory imprinting hypothesis. Smolts taken from their home stream or hatchery shortly before the beginning of their downstream migration and displaced to a second stream returned to the second stream to spawn (Carlin 1969; Donaldson and Allen 1957; Jensen and Duncan 1971; Ricker 1972). Smolts exposed to a synthetic odor can be decoyed to locations scented with this odor during the spawning migration (Cooper and Scholz 1976; Scholz et al. 1976; Sutterlin et al. 1982). Finally, smolts retained past the time of natural downstream migration do not migrate normally, remaining near their release site and non-selectively spawning in nearby streams (Mahnken and Joyner 1973; Peck 1970; Sutterlin et al. 1982).

By definition imprinting involves a single critical period of irreversible learning and once established the imprinted bond is retained for life (Hess 1973). While there is considerable circumstantial evidence to support the olfactory imprinting hypothesis, this evidence is based solely on studies of juveniles during their initial downstream migration. In order to determine if homing is, in fact, based on imprinting, experiments must be conducted on other downstream migratory phases. Although such experiments could not prove the olfactory imprinting hypothesis, they could disprove it if displaced kelts were shown to home to a different release site or overwintering site than their natal stream.

In this study a variation of Carlin's (1969), Mahnken and Joyner's (1973), and Sutterlin et al. (1982) experiments were repeated using Atlantic salmon kelts. These experiments were designed to answer the question: does the learning of "home" stream characteristics occur only during the critical period of

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smolt migration, or does a similar learning process occur each time a salmon migrates to sea?

Materials and Methods

Homing Experiment

In 1982 the basic design of Carlin's (1969) smolt experiments were repeated using seven kelts. The purpose was to determine whether or not kelts would home to their release sites or their spawning–overwintering site, thus disproving the olfactory imprinting hypothesis; or if they would return to their natal stream, thus providing further evidence in support of the olfactory imprinting hypothesis.

In the experimental protocol (diagramed below), kelts were captured in the Big Salmon River, New Brunswick, Canada (Fig. 1) in September 1981. They were tagged with modified Carlin tags of a color and series reserved for Big Salmon River fish and this study, and unique to tags used with other fish released in the previous years. Kelts were spawned by December and held outside through the winter in 5-m uncovered, freshwater tanks (Atlantic Salmon Federation Research Center (ASRC)). Four kelts were released in

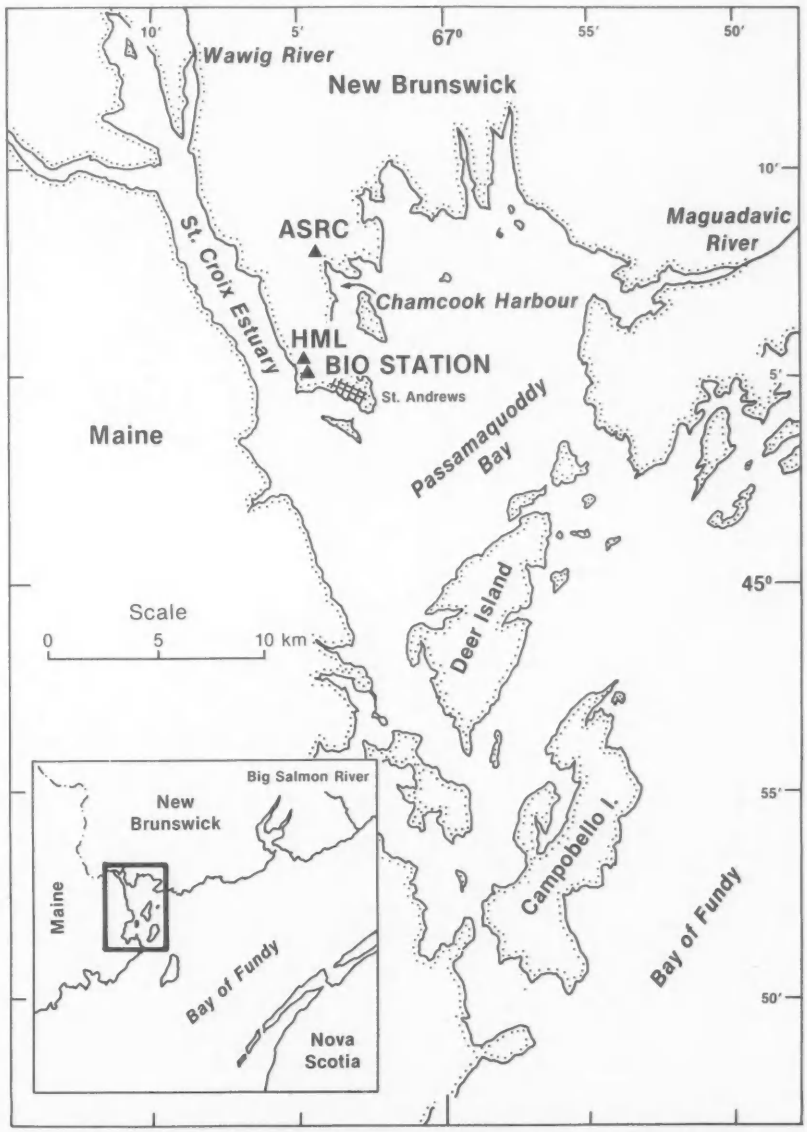
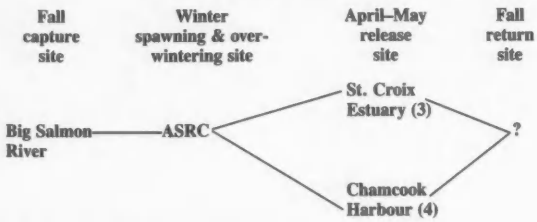


FIG. 1. Study area showing the location where kelts were captured (inset; Big Salmon River), spawned, and overwintered (Atlantic Salmon Federation Research Center (ASRC)), held in the spring (ASRC and Huntsman Marine Laboratory (HML)), and released and tracked (St. Croix Estuary and Passamaquoddy Bay).

Chamcook Harbour and three kelts were released in the St. Croix Estuary.

Normal Release Experimental Protocol

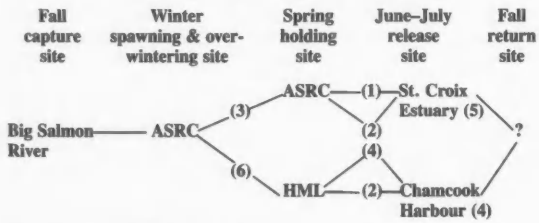


(Number of kelts used per treatment.)

In 1983–84 a modified version of delayed-release experiments described by Mahnken and Joyner (1973), Peck (1970), and Sutterlin et al. (1982) were conducted. Two factors that may have confounded these studies were included in our design: (1) kelts were released at some distance from where they were held during the "critical period" of normal migration, and (2) one group of kelts was introduced to brackish water and one held in freshwater during the period of normal migration.

In the experimental protocol (diagramed below), kelts were captured in the Big Salmon River in September 1982–83, tagged with modified Carlin tags unique to this study and spawned by December. They were held outside through the winter in 5-m uncovered, freshwater tanks at the ASRC. Three of the seven kelts studied in 1983 were held in freshwater at ASRC through the spring migratory period, while all other fish (six) were held in brackish water at the Huntsman Marine Laboratory (HML), before being released in either Chamcook Harbour or the St. Croix Estuary. Delayed release fish were held for varying periods of 1–3 mo after the normal time of migration.

Delayed-Release Experimental Protocol



(Number of kelts used per treatment.)

A variety of methods were in place to document where kelts would return in the fall during the year of release and subsequent years. Kelts returning to their natal Big Salmon River would be observed in diver searches of the downstream holding pools, recaptured by sports fishermen, or recaptured by seining the downstream holding pools. Kelts returning to the major rivers of Passamaquoddy Bay (St. Croix and Magaguadavic) would be captured in the fishway traps at Milltown and St. George for enumeration of upstream migration. Kelts returning to the ASRC (spawning, overwintering or freshwater, spring holding site) would be recaptured in the ASRC weir blocking entrance to the hatchery. Kelts returning to HML (brackish water spring holding site) would be captured in the Department of Fisheries and Oceans Biological Station weir located between the HML's seawater intake and discharge in Brandy Cove. Kelts returning to their release sites would be recaptured in the extensive weir fishery in St. Croix Estuary and Chamcook Harbour. These fish were then to be sonically tagged, released, and tracked to determine if they were homing to their release site. The viability of this method was tested by releasing two returning kelts recaptured in the ASRC weir (released by ASRC as smolts), across Passamaquoddy Bay at Deer Island and sonically tracking them back to the ASRC weir.

Behavioral Observations

Behavioral observations were conducted to determine if delayed released kelts (seven in 1983 and two in 1984) migrated out of the area similar to kelts released at the normal time (seven released in 1982), or if they remained near their release site and spawned in nearby streams like delayed released smolts (Mahnken and Joyner 1973; Peck 1970).

From 1–7 d prior to release, kelts were anesthetised with 2-phenoxyethanol and an ultrasonic tag was inserted through the esophagus into the stomach. Smith Root and Company transmitters (74 kHz frequency and 0.85–3.34 pulses $\cdot s^{-1}$) were used in all but two kelts, which carried Pincock transmitters described by Johnston (1978; 66 kHz frequency and 1–2 pulses $\cdot s^{-1}$). Signals were received using the hydrophone system described by Stasko (1975), although the system described by Clarke (1981) was also used intermittently in 1982.

At least 1.25 h prior to release, kelts were placed in seawater. In 1982 kelts were released by hand or from a dip net. In 1983 and 1984 they were first confined in a floating cage for at least 1 h prior to release.

Kelts were released and tracked under calm seas. Records of fish–vessel positions were made every 15 min by research workers aboard two 10-m+ vessels or smaller 5.25-m vessels, using radar, Loran-C, compass sightings, or dead reckoning. Within 24 h of losing a fish, systematic searches were conducted in the St. Croix Estuary, Chamcook Harbour, and Passamaquoddy Bay to determine if kelts had remained near their release site or had migrated out of the area.

Results

Homing Experiments

In contrast to smolts, kelts released during the normal time of seaward migration did not home to their release sites; nor did they home to their spawning and overwintering sites. However, five of the seven kelts released in late April and early May 1982, did home 150 km to their natal, Big Salmon River by fall. The remaining two fish were not seen again or recaptured.

Of the five returning kelts, one was angled by a fisherman and autopsied, three were observed by divers (one in a lower pool and two several pools further upstream) but not recaptured, and one was observed and seined from the lower holding pool. All four fish were discovered by the survey team on the same day within hours of each other. The two observed in the same pool were seen at the same time and the one observed in the lower pool was still there after seining had been completed. This captured fish was spawned, autopsied and found to be in excellent condition.

In contrast with the kelts released during the normal time of seaward migration, none of the nine kelts released from late May through July, 1983–84 were observed or recaptured in the Big Salmon River (Fisher Exact Probability Test, $P<0.005$). Further, despite the extensive fishing effort expended in

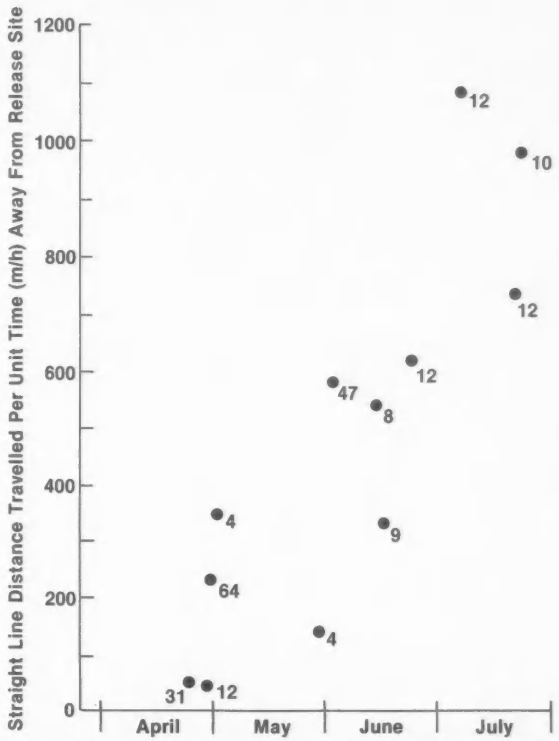


FIG. 2. Straight-line distance travelled per unit time away from the release site (calculated from point of release to point of last observation divided by the hours from release to last observation). Hours from first to last observation ranged from 4 to 64 and are indicated beside each data point.

Passamaquoddy Bay, and despite the locations of weirs off the release sites, the Huntsman Marine Laboratory and the Atlantic Salmon Federation Research Center, and capture nets blocking upstream movement into Chamcook Stream, the St. Croix River, and Magaguadavic River, no kelts released in this study were observed or recaptured in the Passamaquoddy Bay area between 1983 and 1987.

Behavioral Observations

Behavioral observations support the capture data indicating that kelts left the Passamaquoddy Bay. If retaining kelts past their normal migratory period interfered with learning the "home" stream as it does with smolts (Mahnken and Joyner 1973; Peck 1970), then sonic tracking and searches of the Passamaquoddy area were expected to document reduced migratory tendencies and retention of kelts near the release site (Saunders 1977). However, if the "home" stream is only learned during the critical period of smolt migration, then delayed released kelts were expected to travel away from the release site similar to kelts released during the normal period of seaward migration.

It was clear from the behavioral observations that kelts did not remain near the release area or show any lack of migratory tendencies. In fact, the distance travelled away from the release sites in the St. Croix Estuary and Chamcook Harbour per unit time was much greater in June and July than in April and May (Fig. 2). The distance travelled away from the release site per unit time did not appear to be effected by holding the kelts in freshwater or brackish water before release. The distance travelled was based on virtually equal samples taken throughout the 12-h tidal cycle (note hours in Fig. 2) and it was not confounded by any apparent systematic seasonal bias due to greater sampling during any given phase of the tidal cycle.

Kelt behavior changed markedly as the season progressed. Kelts released in April–May were observed by the tracking teams to pause frequently and to drift with or swim at random to the prevailing surface currents. For example, one fish released in April travelled only a few kilometres from the release site in 31 h and another kelt released in the St. Croix Estuary only moved from mid-estuary to the foot of the estuary in 64 h. Net movement was slow and primarily, but not exclusively, dependent on water currents. Kelts released in the early spring were often followed by allowing the tracking boats to drift in the current with the motors off.

All delayed released kelts covered a much greater distance in far less time. Straight line distance travelled away from the release site per unit time increased (Fig. 2) as the season progressed. Thus, instead of milling about the release site as would be expected if their response was similar to smolts, delayed released kelts tended to move away from the release site faster and more directly than kelts released at the normal time of seaward migration.

Discussion

Evidence presented in this study does not support the hypothesis that Atlantic salmon learn the odor characteristics of their

TABLE 1. Seasonal comparison of the results of this study on Atlantic salmon kelts with results from similar, previous studies conducted on Atlantic salmon smolts.

Season	Spring release		Delayed-release experiments	
	Smolts	Kelts	Smolts	Kelts
Fall	Collect eggs and parr various stocks	Capture Big Salmon River	Collect eggs and parr various stocks	Capture Big Salmon River
Winter	Feeding and holding Biological Station or ASRC	Spawning and holding ASRC	Feeding and holding ASRC or Biological Station	Spawning and holding ASRC
Spring	Release St. Croix Estuary; Release Chamcook Harbour	Release St. Croix Estuary; Release Chamcook Harbour	Freshwater holding ASRC; Brackish holding Biological Station	Freshwater holding ASRC; Brackish holding HML
Summer	Feeding Bay of Fundy (Jessop 1976)	Feeding Bay of Fundy (This study)	Release Chamcook Harbour; Release St. Croix Estuary; Feeding Passamaquoddy Bay (Saunders 1977)	Release Chamcook Harbour; Release St. Croix Estuary; ?
Fall	Return St. Croix Estuary Sutterlin et al. 1982); Return Chamcook Harbour (Bailey & Saunders 1984)	Return Big Salmon River (This study)	Return Chamcook Harbour (Clarke 1981); Return St. Croix Estuary (Sutterlin et al. 1982)	Lost at Sea? (This study)

"home" stream during each seaward migration. This study, however, does support the olfactory imprinting hypothesis that salmon homing is based on the one-time irreversible learning (or "imprinting") of the characteristics of their natal stream during the brief critical period of the initial seaward migration following or in association with the process of smoltification.

We have clearly shown that once established the imprinted bond is retained for life and is unaffected by any subsequent seaward migrations. Kelts did not return to either their overwintering or release sites in Chamcook Harbour and the St. Croix Estuary. Instead, they returned only to the site of their initial seaward migration, the Big Salmon River. In contrast, smolts from the Big Salmon River stock raised in freshwater from Chamcook Lake and released in Chamcook Harbour (Bailey and Saunders 1984) or smolts of the Waweig stock, held prior to release in freshwater from Chamcook Lake and released in the St. Croix Estuary (Sutterlin et al. 1982) homed to the release locations (Table 1).

If the time of smolt release is delayed past the normal period of seaward migration, smolts tend to remain near the site of release rather than migrate out to sea (Mahnken and Joyner 1973). In earlier experiments conducted in the St. Croix Estuary (Sutterlin et al. 1982) and Chamcook Harbour (ASF 1986) smolts did imprint and return to their seawater release sites. However, kelts released in late May, June, or July did not remain near their site of release or even remain in Passamaquoddy Bay as predicted by Saunders (1977) for smolts. They were neither captured in the extensive Passamaquoddy Bay fishery nor detected again with the tracking gear during intensive searches. Therefore, the time of seaward migration (spring) or the act of entering seawater does not represent a critical period for learning home stream characteristics in kelts, only for smolts.

Delaying the time of downstream migration may have other effects than those strictly related to imprinting. Delayed released smolts appear to have a greater rate of survival than smolts released during the normal period of seaward migration (Saunders 1977; Sutterlin et al. 1982). However, in this study, delayed released kelts may have had a lower rate of survival, for they were never seen again despite continued observation through 1987.

Further, Saunders (1977) suggests that delaying the time of seaward migration may involve a complex change in smolt migratory behavior, not just a reduction of the distance travelled. This same principle may have some application to kelts. Delayed released kelts appeared to fix a direction of travel earlier and travel farther and faster than kelts released at the normal time of seaward migration in April. In contrast, kelts released at the normal time of seaward migration displayed the same slow, drifting migratory behavior described by Clarke (1981) for smolts released at the correct time in the same waters of Passamaquoddy Bay.

The fact that delayed released kelts did not return to the Big Salmon River may have an underlying physiological cause. While kelts that homed were sexually mature, delayed released

kelts may have lacked sufficient time to restore body reserves. Such a deficiency may have interfered with the onset of sexual maturity and thus their urge to home.

The lack of returns may also be based on migratory behavior. If oceanic migratory progress is dependent on sequentially recognizable information (either innate or learned), the underlying mechanism may be flexible enough to accommodate displacements over distance but not displacements over both time and distance. Since migratory behavior is both time and place mediated (McCleave et al. 1984) then the specific behavioral patterns used by displaced kelts may have been inappropriate for the specific time and location in which they were released.

Whatever the cause, it would appear that like displaced presmolts and smolts, delayed released kelts were unable to find their way back to their natal stream in the calendar year of their release (the normal time for this stock, Jessop 1986) or in subsequent years. This makes the ability of kelts to find their way back to their natal stream after having been spawned, overwintered, and released in a distant site, seem all the more remarkable.

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Age Determination of the Spider Crab *Maja squinado* and the European Lobster *Homarus gammarus* by $^{228}Th/^{228}Ra$ Chronology: Possible Extension to Other Crustaceans

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A method of age determination was developed on carapaces of the spider crab, *Maja squinado* Herbst and European lobster *Homarus gammarus* L., by measuring the natural radionuclides activity ratio, $^{228}Th/^{228}Ra$ in the exoskeleton. This method allows the determination of the time elapsed since the preceding molt of the animal. It was successfully tested on five spider crabs and four lobsters which had molted in captivity and therefore had a carapace of known age. It is probable that the method could, with some reservations, be extended to all marine Decapod Crustacea bearing a well calcified exoskeleton.

Une méthode de datation a été mise au point sur des carapaces d'araignées de mer, *Maja squinado* Herbst et de homards européens, *Homarus gammarus* L. Elle utilise la mesure du rapport d'activité d'éléments radioactifs naturels, $^{228}Th/^{228}Ra$ dans l'exosquelette. Cette méthode permet de déterminer le temps écoulé depuis la mue précédente d'un animal. Elle a été testée avec succès sur cinq araignées de mer et quatre homards ayant mué en captivité, donc portant une carapace d'âge connu. La méthode semble pouvoir être étendue, avec cependant certaines réserves, à tous les Crustacés Décapodes marins à carapace calcifiée.

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The knowledge of the age of an animal is basic for the understanding of individual physiological processes and for the estimation of population dynamics parameters. In the Crustacea, growth by successive molts with a renewal of the complete skeleton each time, prevents a direct age determination by classical methods as on calcified structures (e.g. otoliths of fish and shells of mollusk). In the Decapoda, the indirect methods used to overcome this difficulty (tagging, size frequency distribution, and rearing) all present biases or important restrictions (Burkenroad 1951; Aiken 1980; Hartnoll 1982). It is therefore imperative to have some new approaches to direct age determination.

Radiometric methods, using the short half-life daughter products of the uranium and thorium series have been established (Turekian et al. 1979; Turekian and Cochran 1981; Turekian et al. 1982, 1983) for the determination of molluscs growth rates and more recently tried by Bennett and Turekian (1984), on crabs from a hydrothermal ventfield. They used several couples of radionuclides from the uranium and thorium decay series: $^{210}Po/^{210}Pb$, $^{228}Th/^{228}Ra$, $^{210}Pb/^{226}Ra$, and $^{228}Ra/^{226}Ra$. These methods consider that during the molt, the animal incorporates radionuclides from the surrounding water into the mineral part of its skeleton. The radionuclides decay giving rise to daughter products at a constant rate, following the physical law of radioactivity. The activity ratio between a nuclide and its daughter product is linked to time and therefore gives the time elapsed since the preceding molt or "relative age." The results obtained by these authors do not demonstrate the validity of the method, as it was only applied to exoskeletons of unknown age.

In this work, we validate the method by measuring radionuclide activities on crustaceans which have molted in captivity and therefore bear a carapace of known age. The spider crab *Maja squinado* Herbst, and the European lobster, *Homarus gammarus* L. were used as biological material. As the expected ages were unlikely to exceed 10 yr, the couple $^{228}Th/^{228}Ra$ was used because it is the most appropriate chronometer for this age range.

Materials and Methods

Biological Material

Spider crabs and lobsters sampled at sea, in the Western English Channel, were kept in tanks with a constant flow of

natural seawater. Five spider crabs and four lobsters molted successfully and the date was noted. They were then killed at 0.5, 1.0, 6.0, 6.5, and 15.5 mo after the molt for spider crabs and 1.2, 7.7, and 9.6 mo after the molt for three of the lobsters. The fourth lobster molted a second time, 12.5 mo after the first molt. Its old exoskeleton, or exuvia, was used for the radiometric measurements. For the nine samples, the measurements were performed on the cephalothorax, i.e. carapaces.

Principle of the $^{228}Th/^{228}Ra$ Method

During the period immediately following molting, marine Decapoda calcify their new exoskeleton. They absorb calcium essentially from the surrounding seawater (Graf 1978) as well as radium which is known to follow the chemical behaviour of calcium. The 228 isotope of radium decays within the exoskeleton giving ^{228}Th following the radioactive filiation:

$$^{228}Ra \xrightarrow[5.76y]{\beta} {}^{228}Ac \xrightarrow[6.13h]{\beta} {}^{228}Th \xrightarrow[1.91y]{\alpha} {}^{224}Ra$$

^{228}Th accumulates with time and the activity ratio $^{228}Th/^{228}Ra$ will lead to an age according to the following equation:

$$(1)\quad A_{Th}/A_{Ra} = \frac{\lambda Th}{\lambda Th - \lambda Ra}[1 - exp\,(\lambda_{Ra} - \lambda_{Th})t]$$

where A_{Th} = activity of ^{228}Th, A_{Ra} = activity of ^{228}Ra, λ_{Th} = decay constant for ^{228}Th ($0.36\ y^{-1}$) (Lederer and Shirley 1978). λ_{Ra} = decay constant for ^{228}Ra ($0.12\ y^{-1}$) (Lederer and Shirley 1978). t = age of the exoskeleton (years).
Equation (1) can be written more simply:

$$(1')\quad A_{Th}/A_{Ra} = K\,[1 - \exp\,(-a \cdot t)],$$

where K = transient equilibrium value of the $^{228}Th/^{228}Ra$ couple ($K = 1.50$) a = time constant of the $^{228}Th/^{228}Ra$ couple ($a = 0.243\ yr^{-1}$). The measurement of the ^{228}Th and ^{228}Ra activities in the exoskeleton thus gives the age of this exoskeleton, i.e. the time elapsed since the molt:

$$(2)\quad t = -1/a\ \mathrm{Ln}\ (1 - 1/K \cdot A_{Th}/A_{Ra})$$

from which:

$$(2')\quad t = -4.12\ \mathrm{Ln}\ (1 - 0.669\ A_{Th}/A_{Ra}).$$

This equation will effectively give the time elapsed since the molt if the three following assumptions already established by Bennet and Turekian (1984) in their crab work hold true:

(1) The calcification and therefore the incorporation of ^{228}Ra is rapid compared to the ingrowth of ^{228}Th, the time of molt is thus $t = 0$.

(2) After the calcification, the exoskeleton is a closed system, i.e. there are no chemical exchanges with the environment.

(3) At $t = 0$, the ^{228}Th activity in the exoskeleton is zero, i.e. there is no recycling of the ^{228}Th which was present in the organism during the preceding intermolt.

It should be noted, with the second assumption, that the activities of the radionuclides in the exoskeleton are not affected by the death of the animal. Equation (2) is therefore also valid during the delay between the sampling time and the time of measurement. The age at the sampling time is thus simply calculated by deduction of this delay from the measured age.

Experimental Techniques

Sample Pretreatment and Chemical Separation Procedure

The carapaces, specially those of spider crabs, have a very complex and wrinkled surface structure and must be carefully cleaned before analysis, to remove sand and clay which are rich in radionuclides (e.g. the ^{228}Th content of 30 mg of clay is approximately 20% of the ^{228}Th of a 15 g, 6-mo old, spider crab carapace). The carapace is brushed with an electric toothbrush and its cleanliness verified under a binocular microscope. Epifauna attached to the external surface of older carapaces must also be scraped off.

After all external organic matter has been removed, the carapace is crushed to facilitate the chemical dissolution. Owing to the low level of ^{228}Ra specific activity (typically between 0.1 to 0.3 $dpm \cdot g^{-1}$), a weight of 10–30 g of carapace was used for analysis.

The clean sample is introduced into cold 7N HNO_3 (spiked with ^{230}Th and ^{226}Ra as yield tracers) to dissolve the mineral fraction (essentially $CaCO_3$ and $Ca_3(PO_4)_2$). The remaining organic fraction (essentially chitin) is digested in a hot concentrated HNO_3-$HClO_4$ mixture which ensures the total dissolution of the sample. This solution is evaporated to dryness and the residue taken up in 7N HNO_3. At this stage the radium fraction is isolated by selective coprecipitation with lead nitrate according to the procedure described by Koide and Bruland (1975). A lead carrier (~200 mg $Pb(NO_3)_2$) is introduced and 90% fuming nitric acid added until a final HNO_3 concentration of 75% is obtained. The solution with the insoluble nitrates (essentially $Pb(NO_3)_2$ with some $Ca(NO_3)_2$ + radium) is chilled in an ice bath and allowed to stand for 1 h. The nitrates are centrifuged and the supernatant saved for thorium analysis. The time of precipitation will be taken as zero time for the ingrowth of thorium. The lead nitrate is then heated to dryness and placed in a plastic vial for gamma counting.

Most of the excess nitric acid in the solution containing the thorium is volatilized and 15 mg of iron carrier added. This solution contains phosphate ions in more or less large amounts, depending on the specimen. Phosphates must be removed because they lead to an extremely low chemical yield for thorium. The technique used was derived from that of Toribara and Koval (1967): it consists of coprecipitating thorium with iron hydroxides by the addition of concentrated NH_4OH at pH ~3.8. To ensure a better purification the process is repeated twice then the precipitate is dissolved in 3N HCl and the solution is passed through a cation exchange resin (DOWEX 50 W × 8, 50–100 mesh) as described by Ku (1966). Thorium is selectively adsorbed on the resin, 0.75 M oxalic acid is used to elute the thorium. The oxalic acid eluate is decomposed by fuming with a concentrated HNO_3–$HClO_4$ mixture. The thorium residue is taken up in a 0.1M HNO_3 solution and extracted into TTA (0.4M in benzene). The organic solution is evaporated to dryness on an aluminium foil draped around a brass ring. After being carefully flamed to remove any organic residue, this source is then ready for alpha spectrometry.

When ^{228}Ra activity is too low to be measured by gamma spectrometry or when it is not necessary to obtain the result rapidly, an alternative approach is possible for improving the precision on ^{228}Ra activity measures that is never better than 10–15% by the gamma spectrometric method. It involves an indirect measurement of ^{228}Ra from the ingrowth of ^{228}Th: the lead nitrate, containing ^{228}Ra is stored from 6 mo to 1 yr allowing ^{228}Th to grow towards equilibrium. Then, the $Pb(NO_3)_2$

precipitate is dissolved in 7N HNO_3 and ^{229}Th is added as yield tracer. Fifteen milligrams of iron carrier is introduced and the iron hydroxides precipitated by addition of concentrated NH_4OH to pH 4 to avoid the precipitation of $Pb(OH)_2$. The precipitate, dissolved in 3N HCl, is passed through DCWEX 50 W × 8 resin, and thorium purified by the same procedure as described above.

The occurrence of ^{230}Th activity in the thorium source would mean that some ^{228}Th was coprecipitated with $Pb(NO_3)_2$ at the time of initial precipitation. The ^{230}Th can be quantified using the ^{229}Th spike. An adequate correction is then carried out on the ^{228}Th activity.

In practice, it should be noted that $Pb(NO_3)_2$ precipitation is very selective for radium: residual ^{230}Th is always very low (less than 2% of the initially introduced ^{230}Th activity).

A blank analysis was made following the same chemical procedure as for the samples with the same amount of reagents, carriers, and tracers. The activities obtained from the blanks are 0.015 ± 0.006 dpm for ^{228}Th and 0.030 ± 0.012 dpm for ^{228}Ra (two order of magnitude lower than most of the measured activity of the samples).

The spikes used are natural isotopes, therefore to determine the mean level of activity of these isotopes in the carapaces, some analyses were performed without addition of tracers. The results show that natural ^{230}Th and ^{226}Ra activities are never higher than 3–4% of the added activities.

Instrumentation

The alpha activities of thorium isotopes were counted on silicon solid state detectors coupled to a multichannel pulse height analyser.

The activities of the radium isotopes were measured by gamma spectrometry using a well-type germanium detector (ENERTEC EGPC 20 P11). This low background, high efficiency detector has an active volume of 140 cc, a well diameter of 11 mm, a well depth of 70 mm and a resolution of 2.1 keV at 1332 keV. The detector is coupled with a 16 000 channel analyser (ENERTEC 7183). ^{226}Ra was directly measured from its 186 keV gamma ray and ^{228}Ra deduced from a combination of the count rates at 338.7, 911.2, and 968.8 keV (Erdtmann and Soyka 1979) due to the short half-life (T 1/2 = 6.13 h) daughter ^{228}Ac. Most samples were counted for 3–4 d depending on their activity. The detector was calibrated with several standard solutions mixed with $Pb(NO_3)_2$ powder in the same geometry and weight as the samples.

Precision

Precision on the $^{228}Th/^{228}Ra$ ratio includes:

— uncertainty on the calibration of the tracers solutions, estimated at 2%;

— errors on the gamma counting efficiency which is assumed to be lower than 5%;

— two sigma counting statistical error.

For alpha measurements, a counting time of 3–8 d yields results with about 10% counting statistical error. The precision of a gamma analysis is based on the total activity at a given energy, the background continuum and the blank (blank value resulting mainly from the detector background is generally lower than 10% of the sample activity).

The combination of these errors, as standard errors, leads to an overall precision of 15–25% on the $^{228}Th/^{228}Ra$ ratio.

The precision on the ages declines as the age increases because of the exponential form of the relationship between time and the activity ratio. The best precision is obtained for ages between a few months and 4 yr, where the slope of the curve is steeper.

Detection Threshold

The $^{228}Th/^{228}Ra$ method presented here is limited mainly by the error on the ^{228}Ra determination due to gamma counting statistics. To obtain a two-sigma statistical error of 30%, with a counting time of 4 d and a ^{228}Ra specific activity of 0.2 $dpm \cdot g^{-1}$, as samples weighing 5 g are required.

This weight limit could be lowered by measuring ^{228}Ra via its daughter ^{228}Th using alpha spectrometry, as shown above. Such measurement involves a delay of several months for the ingrowth of the Th daughter from its Ra parent. For example, the same 30% error is obtained for an ingrowth time of 2 yr, using samples weighing only 2 g.

Results and Discussion

The results are given in Table 1 for the spider crabs and in Table 2 for the lobsters. In these tables, the samples are ordered in increasing known ages. The measured ages are in reasonable

TABLE 1. ^{228}Th and ^{228}Ra measurements ($\pm 2\sigma$) for five spider crab carapaces of known age. These give, after calculation, a "measured age" ($\pm 2\sigma$) which is compared with the real age.

Sample No.	^{228}Ra (dpm/g)	^{228}Th (dpm/g)	$^{228}Th/^{228}Ra$[b]	Measured age (mo)	Real time between death and measure (mo)	Age at death time deduced from measurement (mo)	Real age at death time (mo)
1	0.134 ± 0.022[a]	0.015 ± 0.004	0.112 ± 0.034	3.8 ± 1.2	2.7	1.1 ± 1.2	0.5
2	0.128 ± 0.020[a]	0.015 ± 0.003	0.109 ± 0.028	3.7 ± 1.2	2.2	1.5 ± 1.2	1
3	0.145 ± 0.040						
		0.032 ± 0.005	0.222 ± 0.048	7.9 ± 1.8	2.9	5.0 ± 1.8	6
	0.144 ± 0.022[a]						
4	0.145 ± 0.050						
		0.044 ± 0.004	0.250 ± 0.044	9.0 ± 1.8	4.5	4.5 ± 1.8	6.5
	0.176 ± 0.026[a]						
5	0.165 ± 0.050						
		0.059 ± 0.006	0.373 ± 0.068	14.2 ± 3.0	0.3	13.9 ± 3.0	16
	0.158 ± 0.024[a]						

[a]^{228}Ra from the ingrowth of ^{228}Th.

[b]Each ratio is calculated from the more accurate ^{228}Ra measurement that is from the ingrowth of $^{228}Th_{(a)}$.

TABLE 2. ^{228}Th and ^{228}Ra measurements ($\pm 2\sigma$) for four lobster carapaces of known age. These give, after calculation, a "measured age" ($\pm 2\sigma$) which is compared with the real age.

Sample No.	^{228}Ra (dpm/g)	^{228}Th (dpm/g)	$^{228}Th/^{228}Ra$	Measured age (mo)	Real time between death and measure (mo)	Age at death time deduced from measurement (mo)	Real age at death time (mo)
1	0.079 ± 0.012[a]	0.0062 ± 0.0014	0.078 ± 0.020	2.6 ± 0.7	1.3	1.3 ± 0.7	1.2
2	0.237 ± 0.056	0.050 ± 0.006	0.211 ± 0.056	7.5 ± 2.2	1.7	5.8 ± 2.2	7.8
3	0.189 ± 0.034	0.050 ± 0.004	0.265 ± 0.054	9.6 ± 2.1	0.9	8.7 ± 2.1	9.7
4 (exuvia)	0.254 ± 0.048	0.082 ± 0.008	0.322 ± 0.066	12.0 ± 2.8	1.8	10.2 ± 2.8	12.7

[a] ^{228}Ra from the ingrowth of ^{228}Th.

agreement with the real ages (confidence interval of two standard deviations). Nevertheless, if a one sigma standard deviation is taken, some trends must be noted in the behaviour of samples younger than 1 mo and older ones.

Samples younger than 1 mo

Spider crabs 1 and 2 have been killed 15 d and 1 mo after they molted to verify if assumption 3, concerning the absence of ^{228}Th at the origin is fulfilled in very young samples. In fact, the ages found for these two samples are too high. This may be due either to the violation of assumption 3 or to an analytical problem. The measurements are not very precise due to the blank correction which was about 10% of the measured activity, and to the low activity. Nevertheless, the sample for lobster 1, which is also very young and has a low radioactivity shows good agreement between the measured and true ages. Therefore, the ^{228}Th content at t_0 is probably very low.

Samples older than 6 mo

Spider crabs 3, 4, and 5 have had time to finish their calcification. The measured ages are somewhat lower than the true ages (error within a range of 1σ). This may be explained by the fact that the calcification of spider crabs is not instantaneous and that throughout the calcification process, radium may be continuously incorporated in a time of 1–2 mo (Drach 1939). This is significant compared with ^{228}Th half-life, thus assumption 1 is not completely fulfilled. This difference could be modelled, combining the radioactive equation (1′) with an equation describing calcification kinetics. The radiometric ages could then be corrected by a calculated positive value. Unfortunately the calcification kinetics of the Decapoda exoskeleton is very poorly known and, moreover, probably depends on the size of the animals and the temperature conditions.

The lobsters 2 and 3 were allowed to eat their "old" exuvia at the time of their molt 7.8 and 9.7 mo before being sacrified. The measured ages are slightly lower than the true ages, as for the spider crabs and probably for the same reasons (see above). This indicates that there is no incorporation of ^{228}Th from the "old" shell into the new shell and validates hypothesis 3.

Lobster sample (four) which consists of an exuvia, presents the same difference in age as the other specimens, showing that there is no loss of radionuclides during the phenomenon of molt.

One attempt was made for an extension of the method to other crustaceans: one on carapaces of the edible crab *Cancer pagurus* L. and another on the Norway lobster *Nephrops norvegicus* L., they showed ^{228}Ra activity of respectively 0.11 and 0.32 $dpm \cdot g^{-1}$. These values are close to those measured for spider crabs and lobsters: 0.1–0.5 $dpm \cdot g^{-1}$ of carapace.

Conclusions

The $^{228}Th/^{228}Ra$ dating method which was tested for the first time on crustacean of known age, provides adequate results on the spider crab and the European lobster. It may be used on wild specimen of the spider crab to calibrate morphological criteria easily detectable on carapaces of terminal molters for aging specimens aboard fishing boats and for improving management of the natural stocks, or, on species such as lobsters which never reach a terminal molt, to establish a relationship between age and size. It may also offer important opportunities for improving our understanding of the biology and the population dynamics of crustaceans (Le Foll et al. 1987). The method has been experimented in our laboratories on other crustacea, including the edible crab *Cancer pagurus* L. and the Norway lobster, *Nephrops norvegicus* L. It appears that the method would work for all marine decapod crustaceans bearing a well calcified carapace, provided the weight of the carapace sample is higher than a few grams.

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LETTERS AND COMMENTS/ LETTRES ET COMMENTAIRES

Is Recruitment of the Whitefish (*Coregonus lavaretus*) of Lake Constance Already Understood?

Throughout the paper of Eckmann et al. (1988) on "effects of climatic and density-dependent factors on year–class strength of *Coregonus lavaretus* in Lake Constance" there is the underlying assumption that the presented empirical recruitment model causally ("relevant factors ...unraveled") explains a high portion of the variance of the real year–class strength (YCS) of Lake Constance whitefish. This view might be somewhat too optimistic for one or other of the following reasons.

The authors use nominal virtual YCS. Apart from uncertainty in the differentiation of the *Coregonus* forms, and apart from simple sampling error in the experimental fishing, this variable is biased in three directions: Since 1962 fishermen have sold more and more whitefish directly to the consumers; therefore an increasing portion of the total catch remained unreported. Also, the poorer a YCS, the higher is the unreported portion. For the combined effects of these two types of bias, total correction factors (formal $\bar{X} = 2.2 \pm 0.8$), were suggested by Hartmann (1988). Additionally, the virtual YCS neglects natural mortality. Through these biases of YCS the estimates of whitefish stock are also biased. Measurement errors in variables can lead to misjudgement concerning the existence of a stock–recruitment relationship. Stock–recruitment data without estimates of measurement-error variance are "meaningless and misleading" (Walters and Ludwig 1981). In view of the various sources of bias of nominal YCS it would have been wise to leave undecided whether the sizes of real YCS changed during the past half century, including a period of eutrophication.

Because even the transformed YCS and the stock size are not normally distributed (chi-square test and K-S test; 10% level) and because of autocorrelation in the indepedent "larvae stocked" and in the residuals (Walters 1985) of predicted YCS ($r^2 = 0.64$ and 0.35; $n = 20$ and 21; 0.1 and 1% level of significance), the statements on the level of statistical significance and on confidence limits have to be treated with some reserve. Calculations with transformed variables do not indicate to what extent the original variance is "explained" by the model. Also in case of multiple (rotating) testing of different hypotheses the significance level of the final best-fit regression is lower than indicated by the formal "adjusted r^2" (Shephard et al. 1984). The model tends to overestimate a poor YCS and to underestimate a rich one (5% level of significance).

The trend-affected independent variable "number of larvae stocked" may be for example just a substitute of "larvae hatched in the lake" because both depend on the trend-affected weight and age composition of stock. Also the quality of stocking material may have been increased through improvement of breeding techniques. It should be kept in mind that the 3-yr running mean of numbers of stocked fry increased eight times since the 1960's while the nominal YCS does not show a significant trend.

Additional to the point of view of Goodyear and Christensen (1984), effects of stock on recruitment cannot be ruled out by linear regression. Statements by Eckmann et al. (1988) are contradictory: "no stock–recruitment relationship could be detected" versus "conspecifics ...have a negative influence" and "negative relationship between successive year–classes."

TABLE 1. Selected recruitment models on the whitefish (*Coregonus lavaretus*) of Lake Constance. + = relevance of independent variable assumed or suspected; − = irrelevance of independent variable assumed or suspected.

	Months	Wetzlar 1983	Hartmann 1983	Eckmann et al. 1988	Hartmann 1988
No. of cases		16	19	21	23
Adjusted R^2		0.763	0.788	0.836	0.834
No. of independents		4	2	5	4
Precipitation	IV/V				+
Sunshine	III			+	
Sunshine	IV	+		+	
Wind	IV			+	
Wind	IV/V		+		
Temperature	IV	+		+	
Temperature	IV/V		+		
Oxygen	II	+		−	
Plankton	IV	+		−	
Plankton	IV/V				+
Fry stocked		+		+	+
Whitefish stock	I	−		+	
Fish stock		−			
Whitefish growth					+

Biological relevance and causality cannot be proved by an empirical model based on time series of backward-field observations. Such a regression does not identify irrelevant ("evidence that zooplankton is not ...decisive ") or "relevant factors," nor does it make causality of population dynamics directly understandable. At best it serves to formulate a new hypothesis, as Sissenwine (1984) and many others have pointed out.

There is not that much unique in the Eckmann et al. (1988) model in respect to process orientation, combination of physical and biological variables, or formal statistical significance (Table 1). Among the modellers of recruitment of the Lake Constance whitefish (Table 1) there are two schools distinguishable: one uses the meteorological data of April while the other one uses those of April plus May. For example the r^2 of the simple relationship YCS/water–temperature is 0.27 in the set of models of Eckmann et al. (1988), (using April temperature) and 0.53 in a regression using temperatures of April–May. If the outlying pair of data for the year 1974 is taken from the data set (problem of inhomogenity) the significance falls below the 1% level ($n = 22$) for the regression YCS/April temperature. Therefore, we should be less sure that April temperature "is the key factor for... YCS."

Independent from its aim, such an empirical model based on backward time series should be validated, e.g. by testing its prognostic capacity. The model, by partial extrapolation, expects numbers of about 0.4, 2.2, and 1.3 million for the YCS 1983–85 while the observed (and from the catches expected) values are 0.1 million for each of the three year–classes. As a potential source of the prognostic uncertainty the larval kills described by Eckmann et al. (1988) should have been considered. Also, in a discussion on temperature effects on survival of whitefish larvae, the observation that the larvae snap more successfully for prey in warmer water, as argued by Braum and Quos (1981) in context with year–class success of the whitefish of Lake Constance, should not have remained unmentioned.

According to Hahn and Shapiro (1966) a multiple regression should be regarded as a means to an end rather than as an end in itself. Its result should be treated with caution and modesty

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Response to Hartmann

The comment on our paper claims to reveal several errors in the statistical procedures adopted by us. We shall first deal with these criticisms of our model, following the sequence of statements in Hartmann's comment, and then focus upon the general reproach that we provided causal explanations for year–class strength (YCS) variation by multiple linear regression analysis.

We agree that an increasing fraction of professional fishermen's harvest is not registered in official statistics. Unfortunately, Hartmann's correction factors do not provide a solution to this problem, because the derivation of these factors (Hartmann 1988) is largely uncontrollable due to lack of precise data. Furthermore, in his paper it remains unknown which factor was applied to which year. Hence, we preferred to use original data. Although Hartmann maintains the contrary, ln-transformed YCS in our data set are normally distributed range of ln(YCS): 4.543–8.403, divided into eight classes of 0.5 width each, Kolmogoroff-Smirnov-test: $\hat{D} = 0.12 < 0.26 = D_{(21:0.1)}$). The Shapiro-Wilk statistic, W, yields the same result.

Of course autocorrelation exists in the independent variable ln(*larv*), because stocking efforts have been increased since the 1960's. But we performed usual regression analysis and not analysis of functional relationships where another set of assumptions pertain (Kendall and Stuart 1979). Hence, the only requirement is that $\epsilon \sim N(O,\sigma^2)$ (Draper and Smith 1966). Therefore, autocorrelation in independent variables does not affect reliability of the model.

Testing our model for autocorrelation of the residuals by the Durban-Watson test statistic gives an inconclusive result for first order autocorrelation. Further analysis by Yule-Walker and maximum-likelihood method showed that there is no significant autocorrelation for time lags of 1, 2, or 3 yr.

We used the logarithm of YCS as dependent variable because it is a reasonable assumption that independent factors influence YCS multiplicatively: e.g., rough weather conditions in spring result in low larval growth rates and consequently a higher proportion of larvae will die, but not a fixed absolute number. Afterwards, estimates of ln(YCS) were retransformed to allow comparison with observed YCS (cf. our figure 1). The potential bias introduced by transformations is "qualitatively obvious and at the same time scientifically irrelevant" (Box and Cox 1982).

The next argument refers to multiple testing of hypotheses and significance of adjusted r^2 values. The latter value is the fraction of total variance which is accounted for by the model, using the complete data set of 21 yr. The three independent tests of the model using jackknife statistics have no influence on this value. Hartmann's argument would apply for example in the case of multiple comparison of means, where level of significance decreases with number of pairwise comparisons, but this has nothing to do with the methods used in our study.

Our model ($n = 21$) does not show a tendency to overestimate poor and to underestimate rich year–classes (regression of residuals on observed values, $\hat{r} = 0.35 < 0.43 = r_{(19;0.05)}$). Such

a trend, which is barely significant ($\hat{r}=0.44>0.43=r_{(19;0.05)}$), can only be shown when the predicted values from the three jackknife tests are combined (our figure 1). This is simply due to the fact that the model explains a large proportion but not all of the YCS variance.

Number of larvae stocked is speculated to be a substitute for larvae hatched in the lake. During spawning time, fishing is allowed for 2–4 d only and fertilized spawn is delivered to the hatcheries. Under rough weather conditions, catches can be too low to fully utilize all hatchery capacities, no matter how many spawners are present in the lake. On the other side, once all hatcheries are used to capacity, no more eggs can be incubated in order to make their number proportional to the amount spawned in the lake. Therefore, little correlation between number of larvae stocked and larvae hatched in the lake is to be expected.

Improvement of breeding techniques mentioned by Hartmann presumably refers to incubation in cold water in order to delay hatching of larvae. This technique has been used on Lake Constance for several decades. A considerable increase of cold-breeding capacity, however, took place only during the last few years by reconstruction of swiss hatcheries in 1981 and 1987 and by opening of a new hatchery in 1987. Additionally, in order to detect possible positive trends during the 21 yr under consideration, we have evaluated the influence of soluble reactive phosphorus concentrations (column SRP in our table 1) and of date (not mentioned in our paper) on ln(YCS). We could detect no such trends.

In contrast to YCS, the 3-yr running mean of number of larvae stocked is said to have increased eight times since the 1960's. In fact, it increased by a factor of six (cf. last column of our table 1). More seriously, the argument in our eyes reveals a misunderstanding of multiple regression analysis. The relationship between the dependent variable and an independent factor, which accounts for an important portion of variance, might become visible only after the influences of other factors have been taken into account. We explained that this was the case for the variable ln(*larv*) (page 1090 bottom, left column).

Effects of stock on recruitment cannot be ruled out by linear regression analysis. This is perfectly true and hence we explicitly formulated that "no stock–recruitment relationship could be detected." Furthermore, this is by no means contradictory to the argument about the influence of older conspecifics on YCS (cf. our definitions of COMPET and of spawning stock on pages 1090 bottom, right column, and 1091 top, left column).

The two "schools" of YCS modellers on Lake Constance obviously agree on the importance of meteorological influences on YCS of whitefish. However, it is open for discussion how these influences are best quantified (precipitation, water temperature, sunshine), and which months are to be considered (April, April plus May (in fact, we used March plus April)). We have disclosed the reasons for our approach. Having provided good statistical evidence for the importance of certain factors, we suggest that causal relationships are more easily revealed by specific measurements and experiments rather than by further statistical analyses.

Next, a test of the predictive capacity of the model is asked for. It was performed by jackknife statistics and results were shown in our figure 1. Further predictions of YCS for the years 1983 and 1984 from the general model are 336 000 and 1 810 000, respectively (not 400 000 and 2 200 000). By now, these estimates can be compared with observed YCS: while the estimate for 1983 is close to the observed value (100 000), the estimate for 1984 is wide of the mark (100 000). Leaving aside that one outlier is fully acceptable in a 23-yr data set, this observation should be considered a stimulus for future efforts to better understand YCS dynamics, rather than for deploring the poor prognostic capacity of the model which we had explicitly stressed in our paper (last paragraph on page 1092).

The general reproach in Hartmann's comment, that we attempted to causally explain YCS variance by our model, must be rejected. We suggested possible ways in which independent variables might influence YCS. From this concept, testable hypotheses were derived which must now be tested in experimental studies. Along these lines we began to study for example the distribution of coregonid larvae (Eckmann 1988) and growth of coregonid larvae and juveniles by otolith analysis (Eckmann and Pusch 1988). We think that this is an appropriate way to improve our understanding of YCS variations which may then be expressed in improved models — R. Eckmann and U. Gaedke, *Limnological Institute, University of Constance, P.O. Box 5560, D-7750 Konstanz, Germany.* (J9936)

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